TISCIA

an ecological journal

Vol. 31. (1998)

Contents:

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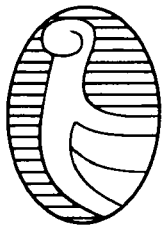
TISCIA



an ecological journal

Vol. 31. (1998)

ISSN 0563-587 X

SZEGED

This volume is sponsored by

National Scientific Research Fund
OTKA Grant No. T 020 149 and
OTKA Grant No. T 025 335
Department of Ecology, József Attila University

TISCIA 31, 3-12

INTERSPECIFIC ASSOCIATIONS IN DIFFERENT SUCCESSIONAL STAGES OF *BRACHYPODIUM PINNATUM* GRASSLAND AFTER DEFORESTATION IN HUNGARY

K. Virágh and S. Bartha

Virágh, K. and Bartha, S. (1998): Interspecific associations in different successional stages of *Brachypodium pinnatum* grassland after deforestation in Hungary. — *Tiscia 31, 3-12.*

Abstract. At the border of the Hungarian Central Mountain Range and the Hungarian Great Plain *Brachypodium pinnatum* is a dominant component of the herb layer of *Quercus pubescens* oakwood. In Hungary, *Brachypodium* grasslands are of very high diversity and natural conservation value because they preserve many elements of the original forest-steppe flora. During the secondary succession after deforestation xeromesophilous *Brachypodium pinnatum* community develops and gradually turns into xerophilous grasslands.
Spatial organization and compositional differentiation of *Brachypodium pinnatum* communities were studied in three stands representing their early, middle, and late secondary successional phases. Presence/absence of species were detected in 20×110 grids of contiguous 5×5 cm micro-quadrats, and analysed by using information statistics.
Early phase was characterized by a coalition of mesic species. Xeric and mesic grasses formed coalition in the middle phase but they were segregated in the late successional phase. However, the pattern of species replacement was diffuse and gradual during the transformation process.

Keywords: information theory, spatial pattern, xeromesophilous grasslands, fine-scale spatial organization, species coalitions

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Introduction

Statistically determined associations between species and species groups are considered to be an important feature of a plant community (Kershaw and Looney 1985).

Analysing the spatial pattern of individual species in natural and disturbed communities has been still very frequent, and interest in this topic has been continued since the pioneering work of Greig-Smith (1952,1961), Hurlbert (1969) and Kershaw (1959, 1960, 1963). While in the „golden age" of pattern analysis about 20 years ago (Greig-Smith 1983, Kershaw 1973, 1985, Schluter 1984) at most one and two-species patterns were studied, recently multispecies patterns (e.g. Bartha 1992, Juhász-Nagy 1976, 1984, Podani *et al.* 1993, Dale 1991, 1995) and coalitions or functional groups have been received considerable attention (Wilson *et al.* 1994, Bartha *et al.* 1995). Several authors emphasized the importance of frequency changes of significant interspecific associations in successions (O'Connor and Aarssen 1987, Leps and Buriánek 1990, Matus and Tóthmérész 1990, Myster and Pickett 1992 and Margóczi 1995). Van der Maarel stressed in one of his reviews (1996) the ecological significance of time sequence of observations and spatiotemporal pattern analyses.

Recently increasing evidences suggest that complex patterns of vegetation and species populations exist at a range of spatial and temporal scales. Great stohastic spatiotemporal variability in distribution and abundance of species or species groups was often revealed which was in many interpretations considered to be an inherent stochastic character of successional patterns to support the individualistic and stochastic concept of vegetation. However, there are many results even at fine-scales, which contra-

dict to the individualistic view and show deterministic feature of the relationships between species and populations (Gigon 1996) or non-randomness of pattern of individual species (Turkington *et al.* 1985, Thorhallsdóttir 1990, Watkin and Wilson 1992). Challenges for ecologists to know more about the spatial organization of species during successions have still remained.

In this paper we study the compositional differentiation of a xeromesophilous *Brachypodium pinnatum* community at fine-scale. Transformation of species composition, fine-scale spatial patterns and coalition structures were analysed along a successional gradient characterized by the gradual change of xeromesophilous *Brachypodium pinnatum* community into xerophilous ones.

This work is part of a larger project dealing with vegetation dynamics, as well as species replacement and microstructure changes of *Brachypodium* communities at different spatial and temporal scales.

The main purpose of the present paper is to reveal the differences in the fine-scale structure of local species coexistence in a changing vegetation of different successional stages. We are especially interested in the changes of pairwise associations between species.

Two hypotheses were tested. Whether 1) species replacements are diffuse and random or particular coalition structure is developing, as well as 2) xeric and mesic species are assembled randomly or they are segregated into microhabitats of different light conditions and water availability.

Material and methods

Study site

Field studies were carried out in a local nature conservation area in the north part of Hungary.

The investigated area is located 25 km east of Budapest at the border of the Gödöllő Hills. The area is part of a forest steppe zone at an altitude of 200-230 m above sea level. The climate of the area is intermediate in character between the continental climate of the Great Plain and the subcontinental climate of the hilly-country. The mean annual temperature is 9 °C and the mean annual precipitation is about 600 mm. Brown forest soil of chernozem character is typical on the loess substrate.

The study area was formerly covered by dry *Quercus pubescens* oakwood. Most of it was cut in the early 1900's (Military Survey 1883, 1943). This forest activity resulted in a wide range of habitats in which diverse vegetation types formed by local secondary successions of different directions and rates. Nowadays, remnants of forest, shrub vegetation and a series of grassland communities of xeromesophilous to xerophilous character can be found along the 2 km long northeasterly slopes of the loess valley. For more details about the description of the vegetation and its landscape-level heterogeneity see Fekete *et al.* 1998.

Brachypodium pinnatum plays a central role in the course of secondary succession following deforestation. This species was the dominant component of the sparse undergrowth layer of the former dry oakforest.

The stands of *Brachypodium pinnatum* (forest remnants) have survived for many decades after deforestation. Some of them are able to preserve many shade-tolerant forest species, while the others become saturated by the xerothermic grassland species. Characteristically, the stands of *Brachypodium pinnatum* community of the open and sunny areas became closed and dense after the removal of trees. Gradual abundance decline of *Brachypodium pinnatum* through the secondary succession can be regarded as long term responses to the lack of forest microclimate and tree canopy closure.

Our target object is a xeromesophilous *Brachypodium pinnatum* community, which represents an intermediate stage along a forest - steppe floristic gradient on the study area. It has developed during the secondary succession after deforestation and it is gradually turning into xerophilous communities (Fekete *et al.* 1998).

Three types of the xeromesophilous *Brachypodium pinnatum* community developed during the past 100 years were selected for the present study. They are different floristically and coenologically from each other in various degree, however these „communities" did not receive a separate syntaxonomical status. For convinience, the terms of „community" and „stages" will be used alternatively further in this paper.

These communities are as follows:

Forest-type of *Brachypodium pinnatum* community represents an early phase of secondary succession. It can be found along the edge of *Crataegus monogyna* shrub on slopes influenced by shadow of *Crataegus* plants and also of small groups of white oaks. Coverage of *Brachypodium pinnatum* amounts to 60-70% or more. The stand is dense and closed, where the average height of the sward is about 50-60 cm. A litter thickness is 10-15 cm. It preserves numerous shade-tolerant forest plant species as rests of the earlier forest, whereas the number of steppe plants is very low here.

Transitional-type of *Brachypodium pinnatum* community representing the middle successional

phase is a so-called mixed type of high mesic and xeric species diversity dominated by many dicots and broad-leaved grasses. The sward is of low saturation, with light closure (50-60%). The height of sward is 30-45 cm, the litter thickness is 5-10 cm. Total cover of *Brachypodium pinnatum* is only 15-35%. Many xeric species are favoured by *Brachypodium* canopy thinning. Coverage of *Festuca rupicola* — pioneer of xerothermic grasslands — often also amounts near 25%. The number of steppe species is relatively high approaching to 15-20, and their total cover is sometimes considerable (35-55%).

Steppe-type of *Brachypodium pinnatum* community represents a late successional stage of the gradient from forest to steppe. The height of sward is 30-35 cm, and the litter thickness is only 2-6 cm. It mainly develops on upper part of slopes to S, so its habitat is fairly warm and dry. The forest plants tolerant to shade are strongly suppressed here. Coverage of *Brachypodium pinnatum* considerably decreased and the vitality of this grass is much lower than it was in the former vegetation type, yellowing of leaves can often be observed. Gaps in the sward are significant giving opportunity for colonizing more and more steppe plants. Abundance of *Festuca rupicola* and many other steppe plants is considerable.

Field sampling

We chose physiognomically uniform stands of each community occurring close together in space. They are all surrounded by *Bromus erectus* grasslands, which means a similar coenological environment in the neighbourhood of each stand. The stands of three successional stages represent also a light gradient associated with the declining dominance of *Brachypodium pinnatum*.

At a fine-scale 25 cm^2 contiguous plots were sampled. Presence/absence of species were detected in 20×110 grids of contiguous 5×5 cm microquadrats in June. Vegetative units of all plants rooted in microplots were also counted. For all graminoids vegetative units are defined as tillers. Small seedlings with only young small leaves were not included, since they differ much from the more established plants, as well as from their dynamics (Herben *et al.* 93).

Computerized sampling and data analysis

From the 20×110 grids of presence/absence data computerized sampling were performed (Podani 1984a,b, 1992). Repeating the sampling procedure with increasing sampling unit sizes across a range of scales between 5×5 cm and 5×150 cm, we created a series of 2×2 contingency tables for each pair at each scale. Association between two species was computed from the 2×2 contingency table and it was expressed by their mutual information, I(A,B) (see Juhász-Nagy 1980, 1984, and Juhász-Nagy and Podani 1983 for details of the computation.) Significant associations were detected by Monte Carlo randomization tests. We applied complete randomization (Diggle, 1983) that randomizes completely the positions of individuals (the presences in our case) of each species within the whole grid (Site model, Watkins and Wilson 1992), but keeps the number of species and their frequencies constant, i.e. same as in the field. Significance of observed value can be calculated as probability of the observed value under the null hypothesis, i.e. the proportion of Monte-Carlo randomizations in which the random I(A,B) is more extreme than the observed value. 5000 randomizations were applied in each test. The sign of associations was detected by comparing the sums of the frequency of the diagonal cells in the 2×2 contingency table (comparing a+d to b+c) (Kershaw 1964). According to our experiences (Bartha and Kertész unpublished), beside the interspecific spatial dependence, this method might detect additional significant positive associations due to autocorrelations (i.e. the aggregated patterns of species) as well. When we repeat the analyses at several sampling unit sizes, the interval of spatial scale of significant associations increases due to autocorrelations. Textural constraints also influence these scales (Bartha and Horváth 1987, Tóthmérész and Erdei 1992). The type of randomization applicable to grids does not allow us to separate these effects. Therefore, we did not interpret the scale of associations. After surveying the significant associations at all sampling unit sizes, an association was considered to be positive if it was always positive. If the sign of associations between two species changed with scale, we considered it as negative, because the additional positive association might indicate autocorrelation only. The same technique was successfully applied for successional data by Bartha (1992). Frequency of significant positive and negative associations were calculated for each successional stage (expressed as percentage of the potential maximum, i.e. the number of possible species pairs). To avoid artefacts due to rarity and due to the limited sample size, rare species (with frequency less than 1%) were omitted from the analyses.

Plexus diagrams depicting the significant positive and negative associations (McIntosh 1978)

were displayed in the case of all species and only for the graminoids.

Considering the coenological and ecological affinities of the species we distinguished 3 groups of species (guilds) in our site, such as the so-called forest species (i.e. mostly mesic, shade-tolerant species), the steppe species (i.e. mostly drought-tolerant and light-demanding xeric species), as well as the „indifferent" species. Thus, the significant associations were also evaluated with respect to these 3 species groups, from which changes in the first 2 groups are likely responsible for the outcome of secondary succession.

Results

Textural attributes

All stands are dominated by vegetatively spreading perennial species. Altogether 60 species were detected in the 3 stands. Some textural attributes in 3 stages of succession are presented in Tables 1 and 2.

It is remarkable, that the proportion of rare species (freq.:<1%) is very high accounting for 68, 57 and 58% of the total number species of each of the stands. In general, very few dominant and codominant (freq.:>5%) species (7,8 and 11) occur in all stands. Most of the species appear in the middle successional stage, but many codominant (50%) species are apperant in the steppe-like *Brachypodium* stand (=late successional stage). *Brachypodium pinnatum* appears to be fairly ubiquitous in the forest-like stand (early stage of succession), where its predominance can result the lowest species richness.

The secondary succession can be characterized by the decreasing dominance of *Brachypodium pinnatum*. Its pathway is thought to be affected by the changes in species abundance, pattern of individuals and varying light conditions. A clear trend of decreasing abundance of mesic and increasing abundance of xeric perennial species along the successional gradient is well-expressed (Table 1), such as the changes of the number of light-demanding xeric species from 25% to 54%. As Table 1 shows, there is only a slight decrease in the frequency of *Brachypodium* along the mesic to xeric successional gradient measured in the microquadrats. However, the considerable decrease of its cover, the decreasing height of tillers, and the lower litter thickness found in the Transitional and Steppe-type indicate indirectly the decreasing viability of *Brachypodium* clones exposed to light and drought after deforestation. Note that the abundance differences are much more considerable also in the case of *Festuca rupicola* and *Bromus erectus*, than their frequency values.

Table 1. Some textural attributes in 3 successional stages of *Brachypodium pinnatum* grassland after deforestation in Hungary

	Forest-type	Transitional-type	Steppe-type
total cover	100	130	115
litter thickness	10-15 cm	5-10 cm	2-6 cm
average height of the sward	50-60 cm	30-45 cm	30-35 cm
total species richness	50	60	53
number of frequent species			
frequency % >= 1	16	26	21
frequency % >=5	7	8	11
frequency % >= 10	3	5	6
mesic species (% of total species)	62	52	42
xeric species (% of total species)	25	46	54
cover %			
Brachypodium pinnatum	74.9	35	22
Festuca rupicola	3.6	7.7	15.4
Bromus erectus	23	17.6	20
frequency %			
Brachypodium pinnatum	79	63	52
Festuca rupicola	23	17.6	20
Bromus erectus	5.5	24.7	25

An approximation of the coalition structure with plexus graphs

In the Forest-type community there are only positive associations (27 in total) between the species. The graph is of reticulate character, majority of species is mesic (Fig. 1a,b, Table 3). The mesic grasses (e.g. *Dactylis glomerata*) and dicots (e.g. *Betonica officinalis*) with low frequency appearing in the small openings of the stand are infiltrated (intermingled with) between the more frequent species. No expressed multi-coalition structure is appearent.

The largest number of significant positive (27) and negative (32) associations were detected in the middle successional stage (Fig. 2a,b). Many mesic and xeric species are mixed with each other forming significant associations. Dicots except of tall species with very deep, weel-developed root system (e.g. *Achillea pannonica - Helianthemum ovatum*, *Astragalus onobrychis - Chamaecytisus austriacus*) are usually positively associated, whereas between

Table 2. Abundance hierarchy of the species in 3 successional stages of *Brachypodium pinnatum* grassland after deforestation in Hungary (Percentage frequency of species (>1 %) in the 20 × 100 grids is presented)

Forest-type	
Code of species	Frequency %
BRAPIN	79.5
FESRUP	23.7
TEUCHA	11.2
CARCAR	7.4
POAANG	6.4
BROERE	5.9
ARRELA	5.5
FILVUL	4.5
FALVUL	4
SESANN	3.6
THYPAN	3.5
TRIMON	3.3
PHLPHL	2.4
GALVER	2.2
DACGLO	1.2
BETOFF	1

Transitional-type	
Code of species	Frequency %
BRAPIN	63.1
BROERE	24.7
CARHUM	18.5
FESRUP	17.6
CARCAR	13.9
HELOVA	9.6
ARRELA	7.6
SESANN	6.7
ACHPAN	4.8
TRIMON	4.1
EUPPAN	4
DACGLO	3.3
TEUCHA	3.2
CAMRIT	3.1
PIMSAX	3
MEDFAL	2.9
KOECRI	2.8
FILVUL	2.8
CHAAUS	2.7
ASTONO	1.7
VIORUP	1.6
PHLPHL	1.5
SILVUL	1.1
CENSAD	1
AGRREP	1
BRIMED	1

Steppe-type	
Code of species	Frequency %
BRAPIN	52.4
BROERE	25.8
FESRUP	20.3
CARCAR	12.6
FILVUL	11.6
THYPAN	10.5
CARHUM	9.2
SESANN	8.6
TEUCHA	8.4
TRIMON	5.7
PHLPHL	5.3
BOTISC	3.6
MEDFAL	3.1
AGRREP	2.5
KOECRI	2.4
THLJAN	1.7
CHRGRY	1.6
DACGLO	1.5
CAMROT	1.2
ARRELA	1
HELOVA	1

Table 3. List of species indicated in the plexus graphs

Name of species	Code	Guilds	Name of species	Code	Guilds
Achillea pannonica	ACHPAN	xeric	*Festuca rupicola*	FESRUP	xeric
Agropyron repens	AGRREP	xeric	*Filipendula vulgaris*	FILVUL	mesic
Arrhenatherum elatius	ARRELA	mesic	*Galium verum*	GALVER	mesic
Astragalus onobrychis	ASTONO	xeric	*Helianthemum ovatum*	HELOVA	xeric
Betonica officinalis	BETOFF	mesic	*Koeleria cristata*	KOECRI	xeric
Bothriochloa ischaemum	BOTISC	xeric	*Medicago falcata*	MEDFAL	xeric
Brachypodium pinnatum	BRAPIN	mesic	*Phleum phleoides*	PHLPHL	xeric
Briza media	BRIMED	indifferent	*Pimpinella saxifraga*	PIMSAX	indifferent
Bromus erectus	BROERE	mesic	*Poa angustifolia*	POAANG	mesic
Carex caryophyllea	CARCAR	indifferent	*Seseli annuum*	SESANN	indifferent
Carex humilis	CARHUM	xeric	*Silene vulgaris*	SILVUL	indifferent
Centaurea sadlerana	CENTSAD	indifferent	*Teuchrium chamaedrys*	TEUCHA	mesic
Chamaecytisus austriacus	CHAAUS	xeric	*Thlaspi jankae*	THLJAN	xeric
Chrysopogon gryllus	CHRGRY	xeric	*Thymus pannonicus*	THYPAN	xeric
Dactylis glomerata	DACGLO	mesic	*Trifolium montanum*	TRIMON	indifferent
Euphorbia pannonica	EUPPAN	xeric	*Viola rupestris*	VIORUP	xeric
Falcaria vulgaris	FALVUL	indifferent			

graminoids and between graminoids and dicots both positive and negative associations prevail. A lot of relatively rare species with low frequency also play a role in developing the complicate association structure of this type. We stress here the importance of positive associations of some xeric graminoids, such as *Festuca rupicola, Carex humulis, Koeleria cristata* with other graminoids and dicots, as well.

In the Steppe-type *Brachypodium* stand a complex association structure among the species is also peculiar, similarly to the former community (Fig. 3a). The number of positive and negative associations is near the same, but both are less, than in the middle stage (17 +, 18 -). It is important that between the perennial graminoids only negative associations appear with one exception (Fig. 3b). It is very likely that the growth habit of grasses partly accounts for the negative values. In this late successional stage mostly xeric species form coalitions and strong spatial segregation of graminoids is characteristic. The commuinty may be divided into 2 coalitions. *Bothriochloa ischaemum, Seseli annuum,*

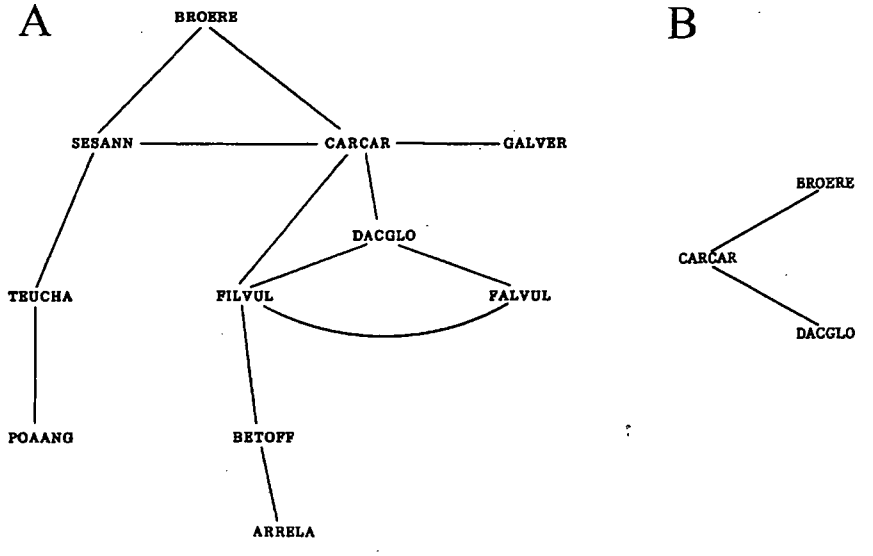

Fig. 1. Plexus diagram for species of an early successional Brachypodium coenostate (significant pairwise associations (p: < 0.01): — positive, ----- negative, A: between monocots and dicots, B: between monocots). (Abbreviations are in Table 3.)

Helianthemum ovatum, Thlaspi jankae, Trifolium montanum are positively associated in the first coalition, while positive associations appear between *Phleum phleoides, Chrysopogon gryllus, Teuchrium chamaedrys* and *Filipendula vulgaris* in the other coalition. These coalitions were separated from each other by many negative associations.

If we consider the significant associations between the 3 groups of species („guilds") differentiated by their ecological requirements (Table 3), much higher number of significant positive and mainly significant negative associations can be found between guilds than within guilds in each commuinty. The greatest differences are in the case of the final stage of secondary succession.

% number of significant associations

	within guilds	between guilds
	(% of within-guild total)	(% of between-guild total)
Forest-type	8.5 (8.5 +, 0 -)	17.8 (16.4 +, 1.4 -)
Transittional-type	11.8 (6.3 +, 5.5 -)	15.9 (8.2 +, 7.7 -)
Steppe-type	7.4 (4.3 +, 3.1 -)	14.7 (6.6 +, 8.1 -)

Discussion

Trends of species associations in succession

A decreasing trend of the frequency of significant associations (standardized by the number of possible species pairs) has been found during the secondary succession. The frequency % changing from 14.2, 12.9 to 10.2% corresponded with the 3 successional stages studied. Our result is in good agreement with the general experience that a declining tendency in the changes of the frequency of significant associations with the successional ages is rather typical (Myster and Pickett 1992). However, no consistent trend in old fields was also pronounced (e.g. Leps and Burjánek 1990).

Coalition structure

In our communities expressed differentiation into well-separated species coalitions could not be found in contrast with the results obtained by Margóczi (1995) and Matus and Tóthmérész (1990) in their natural and grazed sandy communities. Highly complex association structures were revealed in the successional stages of a transforming process of the xeromesophilous *Brachypodium* community. Our grassland types are well-structured with complex multispecies coalitions as compared to the sandy grasslands with relatively simple coalitions of few species.

Most characteristic feature of forming species associations in 3 successional stages of a transforming vegetation

In our communities the number of significant associations was relatively low (10-14%) suggesting diffuse competition between species (Leps and Burianek 1990). Great differences were revealed

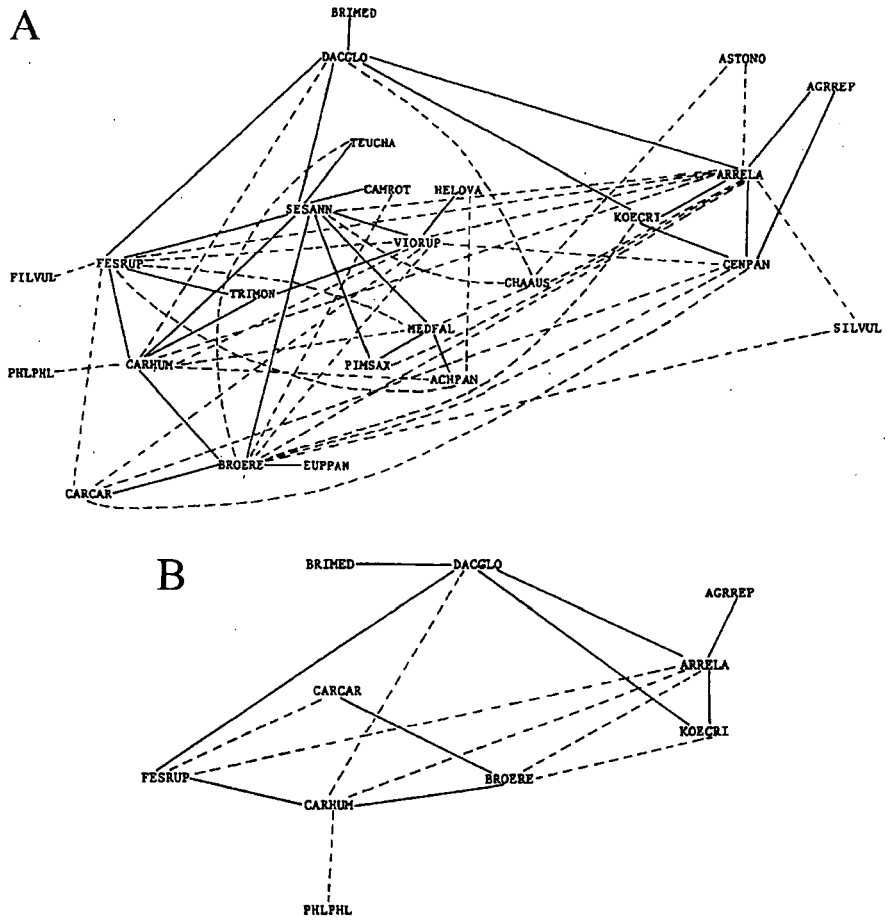

Fig. 2. Plexus diagram for species of a middle successional Brachypodium coenostate. (Explanation for symbols see in Fig. 1 and Table 3.)

how the individual species were spatially assemblaged in the 3 successional stages. The Forest-type community including only positively associated species (mostly mesic ones) was separated from the 2 later successional stages. The most complicated reticulate plexus graph with the highest number of the significant positive and negative associations were detected in the middle phase of succession. Strong segregation of graminoids and development of well-structured coalitions were initiated in the late successional phase.

Plexus graphs analysed varied considerably between successional stages. Early phase was characterized by a coalition of mesic species. Xeric and mesic grasses formed a coalition in the middle phase but the graminoids were strongly segregated spatially in the late successional phase.

We conclude that between communities on a local scale a slow shift of dominance hierarchy took place and habitat selection had also acted. Particular local coexistence structure was typical referring to the different communities. Some exclusion of species combinations was also going on mainly caused by textural and microtopographical constraints. We suggest that the decrease of the dominance and abundance of *Brachypodium pinnatum* modified the micro-environmental conditions (light intensity within a stand, degree of local colonization). Microheterogeneity of the stands influenced forming the species assemblages, as the species or species groups differently preferred the varying microsites and biotic and abiotic conditions in a dense or slightly dense stands of successional stages. The density of individuals, morphology, growth form, limited dispersal and spatial distribution of perennial plants were the most influential factors controlling the coexistence of species.

Thus, answering our first hypothesis, we can conclude that various coalitions are developing in

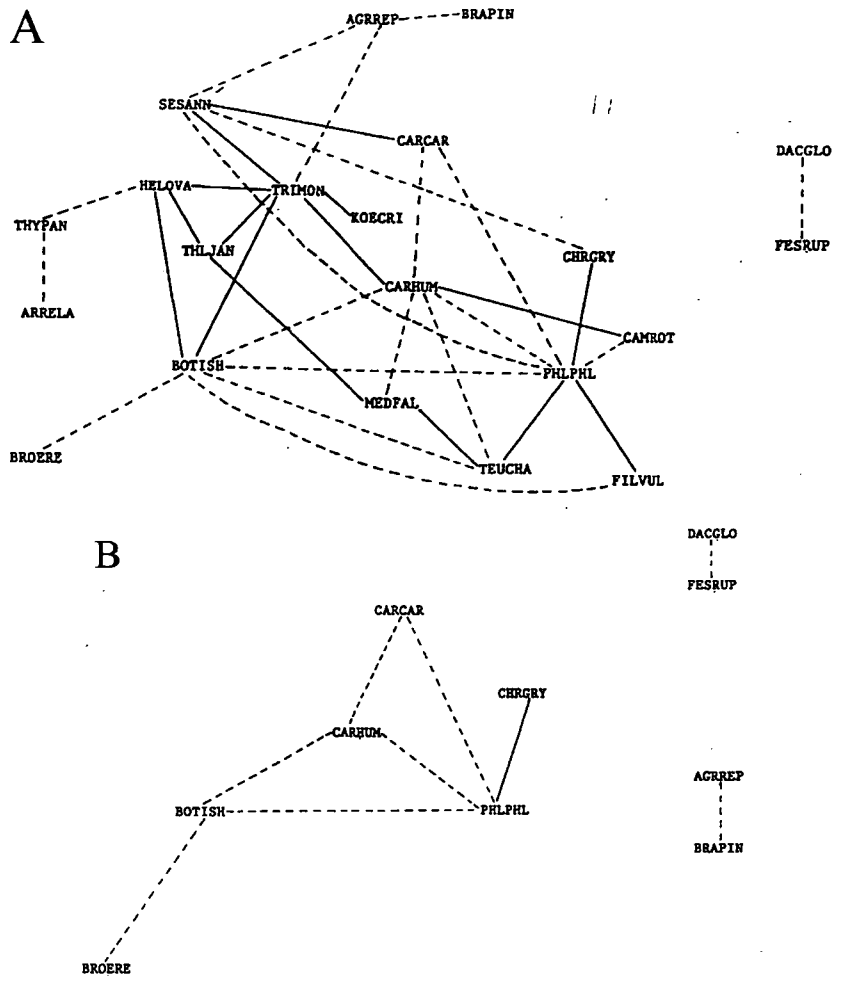

Fig. 3. Plexus diagram for species of a late successional *Brachypodium* coenostate. (Explanation for symbols see in Fig. 1 and Table 3.)

succession. However, it is very likely that pattern of species replacement during the secondary succession is diffuse and gradual instead of a complete replacement of species at stand scale. It was appearent that the species rather showed overlap and continuous transition among the successional stages.

As to the second hypothesis, we can state that in each successional stage most of the species showed non-random fine-scale spatial distribution. Aggregated spatial distribution of many species reflected different spatial microheterogeneity within each stand at fine scale. Forest and steppe species were not completely randomly assembled even at fine spatial scale. We stress that all our communities (states) dominated by perennial species spreading vegetatively were closed of high species saturation, where colonization by seeds were less significant. Fine-scale spatial heterogeneity was mainly caused by growth form of individuals. Dispersal was limited considering that the seeds could reach mainly adjoining microsite of the nurse plants and most propagula were not able to grow in every microhabitat. As a consequence of these phenomena an individual stand was a mosaic of species populations showing particular spatial patterns. Matrix perennial graminoids played an important role in spatial organization. Their segregation in space was obvious. This feature was also found by Thorhallsdóttir (1990) in her community.

Thus, our findings seem to support the non-randomness of species assemblages, similarly with the results obtained by Gigon (1996), Hara (1993), Thorhallsdóttir (1990) and Watkin and Wilson (1992) in their communities. Our results are,

however, partly in contradiction with van der Maarel's carousel model (Van der Maarel and Sykes 1993, 1997, Sykes *et al.* 1994) which assumes that each species can reach and survive each microsite in a community, i.e. the spatio-temporal turnover of species is random. Note that the alvar limestone grassland community studied by van der Maarel was homogeneous, grazed for a very long time and composed by mostly shortlived species. Carousel model might be valid for this species saturated, near the equilibrium community. However, species turnover seems to be well-structured in our spatially heterogeneous transitional communities. We suggest that interspecific spatial associations are dependent on a patchy microenvironment induced by the variation of local population densities, dispersal limitations and limited plant propagations.

Aknowledgements

The research was supported by Hungarian Scientific Research Fund (OTKA T-5032 and T-16225).

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TISCIA 31, 13-17

INDICATION OF HABITAT QUALITY AND ISOLATION BY AUCHENORRHYNCHA ASSEMBLAGES

N. Molnár and Gy. Györffy

Molnár, N. and Györffy, Gy. (1998): Indication of habitat quality and isolation by Auchenorrhyncha assemblages. - *Tiscia 31, 13-17.*

Abstract. The Auchenorrhyncha assemblages of 52 natural and seminatural grassland patches was studied to discover that they are isolated or not. According to cluster analysis based on Renkonen index Auchenorrhyncha assemblages distinguished 5 habitat groups corresponding more or less to the cluster groups derived from the plant associations. Correlations were calculated between similarity matrices based on composition of Auchenorrhyncha assemblages, of plant communities and distances between habitat patches. Demonstration of the distance effect referring to isolation was successful in the habitats that are differing from their surroundings, for example, in case of kurgans enclosed with agricultural areas and grassland patches.

Keywords: habitat fragmentation, Auchenorrhyncha assemblages, insect-plant relationships, nature conservation

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Introduction

Rates of habitat modification are currently so high that virtually all natural terrestrial habitats and protected areas are becoming ecological `islands` in surrounding `oceans` of habitats much altered by human activity. The size of these islands are continuously decreasing, the distances among them are increasing, which may result the isolation of their populations and communities (Gallé *et al.* 1990). The term of isolated habitats means that the migration of organisms between patches is lower than within them. In terms of conservation it is important to recognize the potential danger of the spatial isolation and the degree of the already existing isolation.

The theory of island biogeography dealt first with the isolation of communities (McArthur and Wilson 1967). In case of habitat islands the relation between species number and area is not evident in every assemblages of living organisms, because the habitat islands may have connections with surrounding (mostly agricultural) areas and smaller habitat islands are likely to receive invasive and degradation indicating species (Gallé *et al.* 1990). In several animal groups it was shown that there was higher similarity within habitat islands than among them even if there were different types of habitats inside the habitat islands (Gallé *et al.* 1990). The consequence of the above mentioned facts that the distance among sites may play a significant role in the similarity of communities. According to Krausz *et al.* (1995) the difference of Orthoptera assemblages is determined mostly by the spatial distance of the habitat patches and not by the composition of plant communities.

The main questions in this paper: Does any effect of distance exist in Auchenorrhyncha assemblages of fragmented grassland patches in the Great Hungarian Plain? If it is the case, what is its dependence in the different kinds of habitats? What kind of assemblages are the most endangered by isolation?

Material and Methods

The Auchenorrhyncha assemblages of 52 natural and seminatural grasslands of the Great Hungarian Plain were studied (Table 1, Fig. 1). Detailed data on vegetation and Auchenorrhyncha have already been published (Gallé *et al.* 1990, Györffy and Kincsek 1985, 1988, Györffy 1981),

but were mainly unpublished, original data. The insects were collected by different number of pan traps depending on the patch size (minimum 10). Sampling was carried out in different years with different number of sampling periods, but at least 3 times in a year. As the number of individuals in the samples was very different each time we used relative frequencies of the Auchenorrhyncha species. In the case of plants the relative percentage cover of a species was considered in comparison with the total cover. The pooled number of Auchenorrhyncha species is 177 and of plant species is 361.

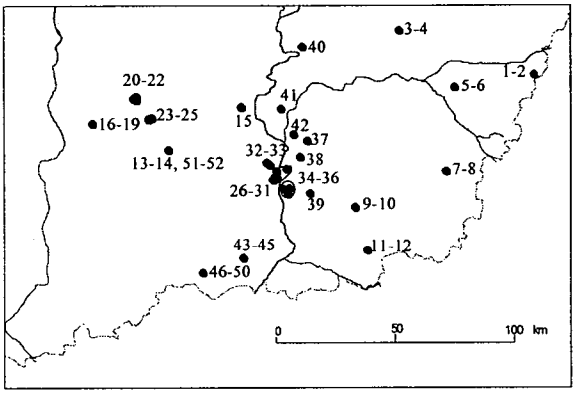

Fig. 1 The 52 habitats in the southern part of the Great Hungarian Plain

We calculated the similarity between sites based on composition of Auchenorrhyncha assemblages and vegetation by percentage of similarities (Renkonen index). Habitat groups were segregated on the basis of the dendrogram, obtained from the result of cluster analysis of Auchenorrhyncha assemblages and vegetation. Correlation was calculated between matrices. On the map we measured the distances between the 52 sites. Also, from these data similarity matrices were composed according to the habitat groups, and correlations were calculated between similarity matrices of Auchenorrhyncha, plants and distances. The establishment of significance level of similarities were performed by SYNTAX program package (Podani 1993).

Results

Five marked clusters were distinguished in the dendrogram of studied habitats based on the composition of Auchenorrhyncha assemblages (Fig. 2). Two sites (18; 9) of extreme sodic vegetation are highly separated from these clusters (cf. Table 1). The first cluster consists of closely connected sites with a vegetation suggesting wet habitats, but there is low similarity between them based on Auchenorrhyncha assemblages (characteristic Auchenorrhyncha species: *Adarrus notatifrons* (KBM.), *Anaceratagallia ribauti* (OSS.), *Doratura homophyla* (FL.)). The second cluster's areas are either loess grasslands that can be characterized by the dominance of *Festuca rupicola*, or grasslands on sodic soil where *Festuca pseudovina* is dominant (characteristic Auchenorrhyncha species: *Rhopalopyx vitripennis* (FL.), *Mendrausus pauxillus* (FIEB.), *Doratura homophyla* (FL.), *Anaceratagallia laevis* (RIB.)). The third cluster with the largest number of objects (19) contains kurgans (cemetery hills) and grassland patches near the river Tisza (characteristic Auchenorrhyncha species: *Artianus interstitialis* (GERM.), *Turrutus socialis* (FL.), *Doratura homophyla* (FL.), *Jassargus obtusivalvis* (KBM.)). These habitats have usually small size and can be considered mostly as patch-like habitats; their vegetation is not really natural. The fourth cluster consists of sandy grasslands (characteristic Auchenorrhyncha species: *Kybos hungaricus* (RIB.), *Jassargus obtusivalvis* (KBM.), *Psammotettix provincialis* (RIB.)). The Auchenorrhyncha assemblages of sodic areas form a separated cluster (it is the fifth cluster: *Lepidio-Puccinellietum, Agrostio-Caricetum distantis, Achilleo-Festucetum pseudovinae* plant associations) (characteristic Auchenorrhyncha species: *Psammotettix asper* RIB.), *Eurysa clypeata* HORV.). The explanation may be due to the extreme habitat circumstances.

On the basis of their vegetation the sodic areas also form a marked cluster (Fig. 3). If we look at the lower numbers of Fig. 3 it can be seen that the arrangement differs from random. Cluster groups derived from the classification of Auchenorrhyncha assemblages more or less correspond to the cluster groups derived from the plant associations. Correlation was calculated between the similarity matrices that served as the basis of the two dendrograms. The value of the correlation coefficient was 0.4131, the significance level was $p < 0.01$.

Comparison of the similarity matrices of the five clusters selected on the basis of their Auchenorrhyncha assemblages was also carried out separately (Table 2). In case of three clusters (2, 3 and 4) significant similarity was obtained between the Auchenorrhyncha assemblages and the vegetation. Between clusters of sodic habitats there was no significant correlation. Its explanation might be that the sodic grasslands are extreme habitats, the vegetation consists of drought-resistant and halophilic species, therefore the plants' salt content is high and the Auchenorrhynchas are adapted to these conditions. Species living in such habitats are

usually polyphagous, so in case of presence of different proportion of plant species the composition of Auchenorrhyncha assemblages are very similar.

The habitat patches in the third cluster can be distinguished by the highly significant correlation between the similarity matrices of Auchenorrhyncha - vegetation, Auchenorrhyncha - distance and even vegetation - distance. The rather small size of these habitats may explain this correlation.

Table 1. The typical vegetation of the 52 sample sites, and the number of plant and Auchenorrhyncha species appearing in the analysis

Habitats	Vegetation	Plant sp.	Auch. sp.
1.	*Succiso-Molinietum*	37	22
2.	*Caricetum elatae*	30	18
3.	*Salvio-Festucetum rupicolae*	20	21
4.	*Agrostio-Alopecuretum pratensis*	26	18
5.	*Peucedano-Asteretum punctati*	37	24
6.	*Populetum canescentis*	20	11
7.	*Artemisio-Festucetum pseudovinae*	10	20
8.	*Salvio-Festucetum rupicolae*	44	25
9.	*Suaedetum pannonicae*	6	6
10.	*Festucetum pseudovinae*	14	17
11.	*Salvio-Festucetum rupicolae*	11	22
12.	*Artemisio-Festucetum pseudovinae*	6	15
13.	*Junipero-Populetum*	40	10
14.	*Festucetum vaginatae holoschoenetosum*	44	16
15.	*Alopecuretum pratensis*	37	35
16.	*Artemisio-Festucetum pseudovinae*	14	22
17.	*Lepidio-Puccinellietum*	4	6
18.	*Bolboschoenus maritimus*	1	2
19.	*Lepidio-Camphorosmetum*	4	6
20.	*Lepidio-Puccinellietum*	14	19
21.	*Agrostio-Caricetum distantis*	29	12
22.	*Festucetum vaginatae stipetosum capillatae*	20	20
23.	*Festucetum vaginatae*	22	13
24.	*Molinio-Salicetum rosmarinifoliae*	33	32
25.	wet *Molinio-Salicetum rosmarinifoliae* hay-field	23	19
26.	*Agropyron repens* (dominant)	10	18
27.	*Poa angustifolia, Arrhenatherum elatius* (dominant)	43	17
28.	*Alopecurus pratensis, Poa angustifolia* (dominant)	31	25
29.	*Festuca pseudovina, Alopecurus pratensis* (dominant)	10	10
30.	*Agropyron repens, Alopecurus pratensis* (dominant)	24	19
31.	*Poa angustifolia, Agropyron repens* (dominant)	15	20
32.	*Poa angustifolia, Achillea pannonica* (dominant)	31	16
33.	*Poa angustifolia, Arrhenatherum elatius* (dominant)	32	22
34.	*Agropyron pectinatum, Stipa capillata* (dominant)	16	41
35.	*Poa pratensis, Agropyron repens* (dominant)	16	42
36.	*Stipa capillata, Festuca pseudovina* (dominant)	13	57
37.	*Bromus tectorum, Agrostis stolonifera* (dominant)	13	36
38.	*Agropyron pectinatum, Festuca rupicola* (dominant)	12	16
39.	*Agropyron repens, Agropyron pectinatum* (dominant)	14	25
40.	*Festuca rupicola, Agropyron pectinatum* (dominant)	17	15
41.	*Phragmites australis, Poa pratensis* (dominant)	19	23
42.	*Festuca pseudovina, Trifolium campestre* (dominant)	9	13
43.	*Achilleo-Festucetum pseudovinae*	14	12
44.	*Achilleo-Festucetum pseudovinae*	14	18
45.	*Lepidio-Puccinellietum*	8	14
46.	*Festucetum vaginatae danubiale*	11	23
47.	*Astragalo-Festucetum rupicolae*	9	32
48.	*Festucetum vaginatae stipetosum*	12	25
49.	*Salix rosmarinifolia*	1	25
50.	*Festucetum rupicolae salicetosum rosmarinifoliae*	8	32
51.	*Festucetum vaginatae danubiale*	17	46
52.	*Molinio-Salicetum rosmarinifoliae*	24	29

Table. 2 Correlations between similarity matrices.

	insects - plants		insects-distance		plants - distance	
cluster	corr. coeff.	p	corr. coeff.	p	corr. coeff.	p
whole	0.4131	<0.01	0.1895	<0.01	0.122	<0.01
1th part	0.0561	n.s.	0.1485	n.s.	0.6509	n.s.
2nd part	0.4704	<0.01	0.0032	n.s.	0.023	n.s.
3rd part	0.4395	<0.01	0.2367	<0.01	0.2203	<0.05
4th part	0.673	<0.05	0.7731	n.s.	0.5174	n.s.
5th part	-0.2115	n.s.	-0.078	n.s.	-0.3108	n.s.

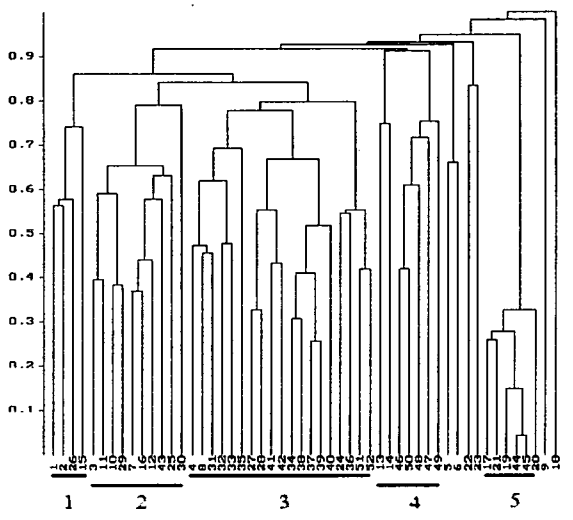

Fig. 2 Dissimilarity of the 52 habitats on the basis of Auchenorrhyncha assemblages (with Renkonen index). Under the figure numbering of the clusters can be seen.

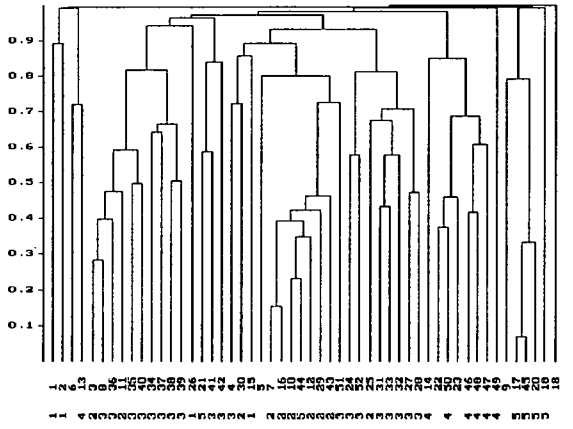

Fig.3 Dissimilarity of the 52 habitats on the basis of percentage cover of vegetation (with Renkonen index). The lower numbers are the numbers established on the basis of the dendrogram of Auchenorrhyncha assemblages.

Discussion

The difference between insect assemblages of two habitats may be caused by many factors. It may indicate different physical conditions, different development of the two assemblages, different form and size of the habitat patches, various kinds of disturbation effects, etc. In case of herbivore assemblages many factors express their effect through the screen of vegetation, in addition the plants are very important as food source, egg laying and shelter, etc. (Crawley 1983, Nault and Rodriguez 1985, Howe and Westley 1988, Denno and Perfect 1994, etc.). Therefore, the knowledge of the vegetation of different habitats is essential when Auchenorrhyncha assemblages are under comparison. After all these the isolation of habitats may be mentioned as a factor causing difference between assemblages.

In the case of the Auchenorrhyncha assemblages the degree of adherence to vegetation is rather high. This is indicated by the identity between the similarity matrices of the plant communities and herbivore assemblages, namely the similar indication features (Gallé *et al.* 1987). The Auchenorrhynchas have `coarse-grained` response, but the grasshoppers show rather `fine-grained` behaviour (Szőnyi and Kincsek 1986). Krausz *et al.* (1995) found that the difference between Orthoptera assemblages less depends on the habitat quality than on the distance of the habitat patches.

The similarity of Auchenorrhyncha assemblages is determined mainly by the properties of the habitat with the mediation of the vegetation. Therefore, relatively high correlation was obtained in case of the initial data matrices between the species composition of the vegetation and the Auchenorrhyncha. In the extremely sodic habitats only few Auchenorrhyncha species are able to tolerate the very salty host plants and the aridity which is typical despite periodic water covering. These assemblages

with law species numbers differ definitely from the others, and we would lose special species groups with the cessation of these kinds of habitats. To verify the isolation is rather difficult here, because species of these habitats with high adaptability cannot or hardly can substitute at all. Similarly extreme arid habitats can be found in sandy grasslands. The Auchenorrhyncha assemblages of these habitats are characterized by stress-tolerant species. The species number is higher, because of the variety of non-characteristic species. Differences are higher, therefore, we suppose the effect of isolation. As the humidity conditions become more favourable, the number of Auchenorrhyncha species increases, whereas in the most humid habitats there are fewer species, but they are more characteristic (mainly Delphacidae).

Kurgans and grassland patches are exposed to invasion of pest species, therefore pseudodiversity may occur, but also edge effect may strongly influence the composition of assemblages. These habitats may be considered as isolated ones. The connections (ecological corridors or stepping stones) between these patches are the least probable. Thus fragmentation of habitats in the Great Hungarian Plain reached the limit that endangers the existence of the most characteristic Auchenorrhyncha assemblages. It is not accidental that the tendency is more expressed in case of Orthopteras which need larger areas (Krausz *et al.* 1995).

Acknowledgement

We would like to express our thanks for the vegetation data to those botanist colleagues taking part in the general assessment of naturalness of habitat types of Kiskunság National Park and Körös-Maros National Park. We are also grateful to Dr. Katalin Margóczi and Dr. László Körmöczi, who kindly provided further vegetation data.

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TISCIA 31, 19-28

STRUCTURE OF ANT ASSEMBLAGES IN A MIDDLE-EUROPEAN SUCCESSIONAL SAND-DUNE AREA

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Gallé, L., Körmöczi, L., Hornung, E. and Kerekes, J. (1998): Structure of ant assemblages in a Middle-European successional sand-dune area. — *Tiscia 31, 19-28.*

Abstract. The species composition, diversity, population interactions and external correlates of ant assemblages are described in different successional plots of a sand-dune area in the Kampinos National Park, Poland. The pooled mean population densities were in the range of 0.018-0.37 colonies/m^2 and increased toward the last successional phase. The species diversity also increased, but there was a diversity decline in the last phase, probably as a consequence of the presence of red wood ant species, which are dominant in the interference competition. The range of a particular species' distribution in different ant assemblages is characterized with its position and breadth in the corresponding PCA factor space. The species number against position histogram is bimodal and differentiates the species of early successional assemblages from that of the mature, well organized communities.

The composition of the ant assemblages was found to be correlated with some structural habitat properties (architecture of vegetation, the number and condition of dead twigs on the soil surface, temperature) and the composition of epigeic fauna. In the competitive network of the early successional ant communities, *Formica cinerea* and *Myrmica rugulosa* have the same rank and both species are subordinated to *Formica truncorum*. The interference interspecific competition has an increasing significance towards the advanced successional stages.

Key words: ants, community composition, succession, diversity, interference competition

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Introduction

The possibilities of the generalization of the results obtained in particular habitats or regions are among the main conceptual and methodological problems of community ecology. A possible tool towards the generalization is the comparison of animal assemblages at different regions to reveal the similarities and dissimilarities both in their composition and in the structuring mechanisms (as illustrative examples on ants, see Andersen 1986a, 1986b, 1992a, Morton and Davidson 1988, Herbers 1989).

Most of the papers, however, that have been published on ant community succession (e.g. Boomsma and Van Loon 1982, Gallé 1981, 1991, Járdán *et al.* 1993, Szujecki *et al.* 1978, Vepsäläinen and Pisarski 1982, Zorrilla *et al.* 1986) concern only particular areas or even habitats. Therefore, it is not really known, whether the phenomena and mechanisms described in those papers are general properties of ant community succession.

This paper reports a part of a series of comparative studies on the succession of ant communities in sand-dune areas along a geographical gradient from Finland to Turkey (for the first results, see Gallé 1990a, 1990b, 1991, 1992, Járdán *et al.* 1993). The aim of this paper is to describe the structure of ant assemblages in successional dune plots in Kampinos National Park (Poland). The main questions addressed are as follows: (1) What is the composition of the ant faunulas in different successional plots? (2) Is there any genetic relation between the ant assemblages of the studied successional plots? (3) Are there differences in spatial patterns of ant populations and assemblages in different successional stages? (4) Is there any trend in the ant species diversity along a successional gradient? (5) Which external factors are correlated

with the distribution of ants among habitats in different successional phases? (6) What is the effect of interspecific competition on the process of organization of ant communities in early stages of succession?

Materials and methods

The field studies were carried out in the Kampinos National Park, near Warsaw (Poland). For detailed ant community surveys, we selected nine plots that presumably represented different stages of vegetation succession. One of them (plot 1) was a bare sand, almost without vegetation; plots 2 and 3 represented initial steps of vegetation succession, with mosses, lichens, some pines and very poor herb layer. The vegetation cover was less than 40%. Plots 4 and 5 were grasslands; plot 6 was a shrubby site in a transitional habitat between a grassland and a pine forest; plot 7 was a young pine plantation, which we expected to belong to the transitional successional stage between grassland and forest; and the two remaining plots were pine forests with (plot 9) and without (plot 8) a high density of red wood ant population. For detailed characterization of the study plots a set of 90 habitat scores were used, in six groups (Table 1).

The density and distribution of ant nests were estimated via grids of quadrates of 16 or 25 m^2 size. The ground was dug to a depth of 20 cm to find all ant nests in those plots which were covered by dense vegetation. Altogether an area of 1035 m^2 was sampled in this way. The position of nests and nest entrances were mapped for further analysis. Spatial distribution of nest entrances, calices and nests were studied with the distance to nearest neighbor method (Clark and Evans 1954) and with grid-pattern analysis of mapped colonies by increasing the size of sample units (Greig-Smith 1983, Körmöczi 1987).

Ordination techniques are useful tools in successional studies (cf. Howard and Robinson 1995). Therefore, the state of each sampled ant assemblage in an assumed successional sere was established by PCA ordination and similarity analysis. Renkonen's percentage similarity function,

$$CR_{ih} = 100\sum_j \min(p_{ij}, p_{hj})$$

and an asymmetric index of similarity formally the same as Levins' function

$$CL_{i,h} = 100\frac{\sum_j p_{ij} p_{hj}}{\sum_j p_{ij}^2}$$

were employed to compute similarities of different assemblages, where $p_{i,j}$ is the relative frequency of jth species in the assemblage i.

Markov chain models are widely used to study the successional relationships of the different stages of ecological systems (Horn 1975, 1976). In the present study, we computed the transitional probabilities between the ant assemblages of the sample plots from their similarity matrix. The Markovian properties of the assemblage sequences were investigated with a chi-square test of the estimate of $-2\ln\lambda$ (Usher 1979, 1987).

The PCA ordination of the individual sampling units on the basis of their ants yielded information on the position and overlap of ant assemblages of the sampled habitats plots. The range of the assemblages occupied by a species, called breadth hereafter and the position of a particular species in the PCA space were computed with similar basic concepts as were employed by MacNally and Doolan (1986). Let w_i is the amount of variance explained by the ith factor and $\overline{x}$ and s_i are the mean and standard deviation of sample units which are occupied by the species in question, then the breadth (B) and the position (P) are defined by these equations:

$$B = \frac{\sum_i \{w_i s_i\}^2}{\sum_i w_i^2} \quad \text{and}$$

$$P = \frac{n\sum_i \{w_i x_i\}^2}{\sum_i w_i^2}.$$

Species diversity was computed by the means of both Shannon-Wiener (Shannon and Weaver 1949) and Simpson-Yule (Pielou 1975) indices. The former was used to characterize the diversities of different successional ant assemblages, and the latter to compute correlation between the different diversities (i.e. plants and ants, vegetation architecture and ants, etc.).

From among the habitat properties (Table 1), for the analysis of vegetation architecture and composition, the coverage values were assessed in grids of 5×5 m cells by eye at different heights and expressed as percentages. The average number of dead twigs on the ground was estimated in 50×50 cm quadrates; the size and condition of twigs were also noted. A set of ten such quadrates were taken at each site.

Soil water content was measured at depths of 5 and 10 cm. The physical composition of the soil was characterized by hygroscopic values (Balleneger 1953). Soil temperature was measured at a depth of 5 cm and that of the air at 40 cm and 200 cm above the

Table 1. Attributes for characterization of study plots

Group	Attributes	No of categories
1. Vegetation architecture	1.1. Whole vegetation cover	1
	1.2. Cover of mosses and lichens	4
	1.3. Cover of plant debris	3
	1.4. Plant cover at 5-15, 15-30.... cm levels	4
2. Vegetation composition	2.1. Relative frequency of predominating plant species	33
3. Size of the plot		1
4. Dead twigs on the ground surface	4.1. Density of dead branches of various sizes and conditions	14
5. Soil and microclimate	5.1. Temperature of soil and of air above soil surface as a difference from air temperature at 2 m height	2
	5.2. S.d. of 5.1.	2
	5.3. Soil humidity at two depths	2
	5.4. Soil hygroscopic value	2
6. Epigeic fauna	6.1. Density of various animal groups collected in pitfall traps	22

ground surface. All temperature measurements were carried out ten times simultaneously in all nine study plots on cloudless days.

Pitfall trap method was employed to establish the composition of ground surface fauna. Fifteen traps were used in each habitat plot for a week. Collected materials were preserved in ethanol (70 %) and sorted at taxonomic group levels (altogether 22 taxa).

External factors that presumably affect the habitat selection and assemblage composition of ants were identified with principal component analysis. Study plots were ordinated in six different factor spaces on the basis of the following attribute groups: vegetation architecture, floral composition, number and condition of twigs on the soil surface, microclimate and soil properties, composition of epigeic fauna, and composition of ant assemblages. The relative position of points representing habitat plots in the PCA spaces were measured with multidimensional Euclidean distances (Pielou 1984), weighted by the variance of PCA axes. We then computed the similarities of the different PCA spaces on the basis of the relative position of points representing sampling plots with nonparametric Spearman's rank correlation. The contribution of single habitat properties to the axes of the PCA ordination factor space of ant assemblages was studied by simple correlation analysis.

Distribution and co-occurrence data are not always reliable for the detection of interspecific competition. Both Alatalo *et al.* (1986) and Hastings (1987) suggested that field experiments (reviewed by Connell 1983, Schoener 1983 and Gurevitch 1992) should be carried out to establish the presence and importance of competition. The direct competitive interactions between different species were therefore studied in bait experiments. We used honey and tinned meat to bait ants. Baits were put on small leaves which were fixed on the soil with small (ca 4×4 cm) pieces of paper sheets and pines. Altogether 285 bait recordings were made and ants were observed on baits in 180 cases. These bait experiments yielded evaluable data sets for the interaction of the *Formica truncorum* F. - *Formica cinerea* Mayr and *F. cinerea* - *Myrmica rugulosa* Nyl. species pairs. In a previous study (Gallé 1991), similar data were obtained on *F. cinerea*, *F. sanguinea* Latr. and *Lasius psammophilus* Seifert. species. In this way we have information on most possible relevant interactions of ant species on the early sand-dune successional stages in North Europe and the northern part of Middle Europe.

Results

Nest densities and species composition

Altogether 22 ant species were collected from the 9 habitat plots (Table 2). The pooled population densities varied between 0.018 and 0.37 nests/m^2. The lowest densities were found in plot 1, which had a bare sand surface, and the highest density data were observed in plot 9, which was a pine forest with a high density of foraging individuals of *Formica polyctena* Foerst.

The PCA ordination of the sampling units yielded the following results (Fig. 1). The ant assemblages of the open habitats (plots 2, 3, 4 and 5) and that of the forests (plots 8 and 9) are segregated along the first PCA axis. The central position of plot no 1 is explained by the fact that since it was an almost bare sand surface, its ant fauna mainly consisted of individuals occurring accidentally without nest. The only nesting species was *Lasius psammophilus*. This poor, single species ant assemblage could be a starting point of ant community assembly in both open and forest habitats. The transitional

Table 2. Density of ant colonies/100 sq m in different study plots. + only workers or * females were collected by hand or in pitfall traps

Species	Plot number								
	1	2	3	4	5	6	7	8	9
Myrmica laevinodis Nyl.			+						*
Myrmica ruginodis Nyl.	+	+	+	+		9.4	+	3.1	15.6
Myrmica rugulosa Nyl.		+	2.9	+	+	1.6	+	1.6	
Myrmica sabuleti Mein.				+					+
Myrmica lobicornis Nyl.	*				+	+	+	+	1.6
Myrmica schencki Em.	+	+		+	+	1.6			
Leptothorax acervorum (F.)						4.7	1.0	1.6	4.7
Leptothorax muscorum (Nyl.)			0.9	+		9.4			*
Leptothorax nylanderi (Foerst.)								3.1	14.1
Diplorhoptrum fugax (Latr.)		+	4.8	+	+	+	4.0	+	
Tetramorium caespitum (L.)	+	+		1.7	4.5	+	5.0		+
Stenamma westwoodi Westw.								+	*
Lasius fuliginosus (Latr.)				*					
Lasius niger (L.)				3.3	1.1		+		
Lasius alienus (Foerst.)	1.8	3.0	1.9	+	1.1				
Formica fusca L.				3.3		6.3	+	4.7	1.6
Formica rufibarbis F.	+						+		
Formica cinerea Mayr		6.0	13.3	+	+	+	13.0		
Formica rufa L.		+						+	
Formica polyctena Foerst.									0.01
Formica truncorum F.							+		
Formica pratensis Retz.	+			+	+		+		
Total	1.8	9.0	23.8	8.3	6.7	33.0	23.0	14.1	37.6

position of plot 6 is in accordance with its vegetation mentioned above. The ant assemblage of the young pine plantation (plot 7) differs from the older, natural forests and situated among the open habitats in the PCA scattergram. The second axis is responsible for the differentiation of grassland ant assemblages from that of other open habitats (Fig. 1).

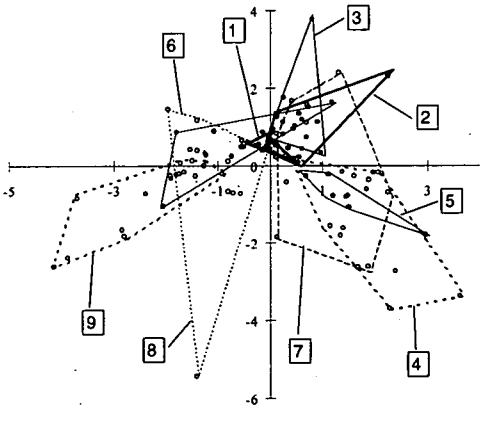

Fig. 1. Scattergram of the pitfall trap sample units of different plots along the two principal axes of PCA factor space on the basis of the species composition of their ant collection.

No significant correlation was observed between the position (P) and the breadth (B) values of the ant species (Spearman rank correlation $r = -0.36$, $n = 21$, $p>0.05$). The species number against P histogram is bimodal (Fig. 2). The species which have lower position values are usually early successional species (e.g. *Tetramorium caespitum* L., *Formica cinerea*, *Diplorhoptrum fugax* Latr., *Lasius psammophilus*). or belong to the transitional assemblages (e.g. *Myrmica lobicornis* Nyl., *Myrmica rugulosa*) and only two species of the third column are the members of "mature", competitively organized ant communities (i.e. *Formica pratensis* Retz. and *Formica fusca* L.) as a rule, but in Kampinos they occupy early successional habitats, too. The most of

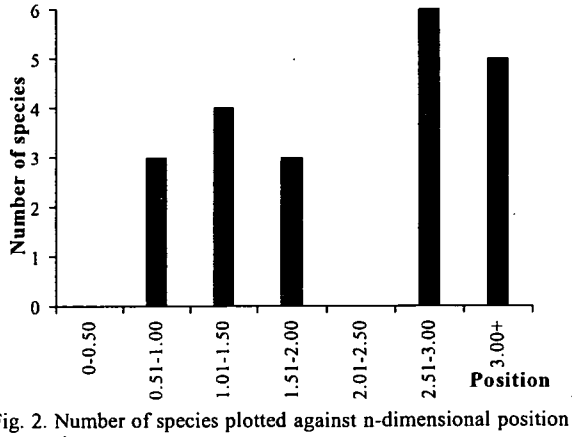

Fig. 2. Number of species plotted against n-dimensional position (see text)

the species having high P values and hence more extreme position in the PCA scattergram (last two columns in Fig. 2) are the members of mature grassland or forest ant communities (e.g. *Myrmica*

Table 3. Factors correlated with PCA axes of ordination of ant communities. |r| = absolute value of coefficient of correlation, p = level of significance

Factors	axis	|r|	p
Total plant cover	I	0.69	<0.05
Dead dicotyledon cover	I	0.75	<0.02
Dead monocotyledon cover	II	0.89	<0.01
Dead pine needle cover	II	0.65	<0.05
Plant cover at 5-15 cm level above soil surface	III	0.67	<0.05
Plant cover at 15-30 cm level	I	0.77	<0.02
Plant cover at 30-50 cm level	III	0.79	<0.02
Dead twigs of different sizes	I	0.74-0.96	<0.05-<0.01
Dead twigs of different conditions	I	0.62-0.84	<0.1-<0.01
One condition class of twigs	II	0.67	<0.05
Soil temperature	I	0.65	<0.06
Temperature in herb layer	I	0.64	<0.07
Four different plant species contributing markedly to herb layer structure	I	0.64-0.71	<0.1-<0.05
Different shrubs and trees	II	0.77-0.89	<0.02-<0.01
Five other plant species	III	0.61-0.71	<0.1-<0.05
Diplopoda	I	0.92	<0.001
Blattodea	I	0.64	<0.06
Gastropoda	II	0.65	<0.07
Chilopoda	II	0.86	<0.01
Heteroptera	III	0.70	<0.05

schencki Em., *Lasius niger* L. and *Formica rufibarbis* F. or *Formica rufa* L., *Formica polyctena*, *Leptothorax nylanderi* (Foerst.), *Leptothorax acervorum* (F.) and *Stenamma westwoodi* Westw. respectively), where the interspecific competition has an important structuring effect (cf. Gallé 1986, 1992).

External correlates

The first three PCA axes of the ant assemblages are correlated with the cover of living and dead plants, the components of the plant architecture, the properties of the dead twigs on the ground surface, the cover of some plant species that contribute markedly to the structure of the herb layer, different shrubs and trees and some epigeic animal groups (Table 3). In addition to the figures in Table 3, slight correlation was found with soil and herb layer temperature, Staphylinoidea, Blattodea (axis I), *Festuca ovina*, and Gastropoda (axis II).

Although these above mentioned factors might be intercorrelated, therefore not all of them are necessarily related with ant assemblages, on the basis of their correlation with PCA axes, we might expect the vegetation architecture, the dead twigs on the soil surface, the physical habitat properties (microclimate and soil), the vegetation composition and the composition of the epigeic animal assemblages, to be those groups of habitat scores that affect the composition of ant assemblages in some ways. These expectations agree with the results of the rank correlation analysis of the relative position of study plots in different PCA spaces in few cases only. It seems that ant assemblage composition is correlated with three groups of habitat scores, i.e. the architecture of vegetation, the dead twigs on the ground surface and the composition of the epigeic invertebrate fauna (Table 4). A table-wide $p<0.05$ significance level is maintained if we ignore the non-significant values in Table 4 (sequential Bonferroni-test, Rice 1989).

Table 4. Rank correlation between PCA spaces of different groups of habitat scores and ant assemblages

Score groups	r	p
Vegetation architecture	0.33	<0.05
Dead twigs in the ground surface	0.69	<0.001
Vegetation composition	0.23	n.s.
Soil and microclimate	0.22	n.s.
Composition of epigeic fauna	0.38	<0.02

Successional pathways and their directionality

The ant assemblages of the different habitat plots can be arranged into a successional sequence on the basis of the PCA ordination (Fig 3). This sequence is supported by the similarity analysis: the similarity values marking the possible successional relations and pathways (continuous lines in Fig 3) or any subset of them are significantly greater than the corresponding remainders (*t*-test, $p<<0.001$ in all cases). The chi-square test of the Markovity of these successional seres is also significant if the p.c. similarity values are used (either *CR* or *CL*) in the tally matrix ($\chi^2 = 2036$, $p<0.001$ and $\chi^2 = 224$, $p<0.001$, respectively). If *CR* and *CL* values are employed as decimals, however, the test result is insignificant, because the function $2\ln\lambda$ depends on the absolute values of the elements of the tally matrix. These absolute values are not independent of

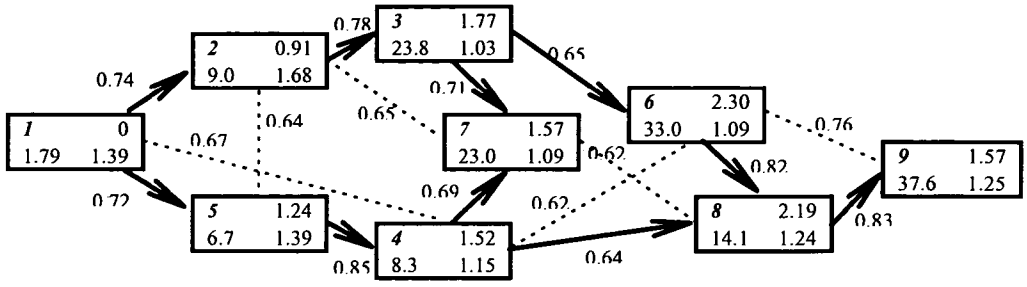

Fig. 3. Probable successional sequence of ant assemblages sampled in different study plots. Upper row in the blocks from left to right: plot number and diversity of ant assemblage; lower row: pooled density of ant colonies and R values of nearest neighbour analysis, respectively

the investigator's decision, therefore, we do not regard this technique as a powerful tool to test the directionality of presumed successional graphs.

The value of correlation between the successional graphs of the ant communities and that of the vegetation is r=-0.0098 (n.s.). Uncoordinated steps between the successional sequence of the vegetation and that of the ant communities were likewise found in other areas (cf. Gallé 1991, Margóczi 1993, Járdán *et al.* 1993).

Diversity

The Shannon-Wiener diversity increases towards the mature stages of ant community succession (Fig 3), but there is a decline in plot 9, representing the last phase. This probably is a consequence of the high density of an aggressive red wood ant species, *Formica polyctena*. The diversity of ant communities is correlated with that of the vegetation architecture (r=0.66, p<0.05); the vegetation composition (r= 0.87, p<0.01); and the epigeic animal communities (r= 0.55, p<0.1).

Spatial patterns

Nearest neighbor analysis indicates that the distribution of ant nests for all species is of random type in plots 3, 4, 6 and 7, which represent grassland, forest edge and young forest successional stages and it is of regular type in the earlier and more advanced phases (Fig. 3). No clear trend in the changes of spatial patterns could be observed in the successional sequence of Kampinos ant assemblages either for the single species populations: the R values vary between 0.65 and 1.85; the majority of them lie in the range of random or regular distribution, and they are independent of both ant species and successional stages.

Interference competition on baits

The direct interactions could be studied on three species, *Formica truncorum*, *F. cinerea* and *Myrmica rugulosa*, from the results of bait experiments. As it may be seen in Table 5, the baits were occupied by ants in the majority of observations (180 observations, >63%). The encounters of different species were recorded in 70 cases (38% of the above 180 recordings). *Formica truncorum* was the most aggressive species, dominating the ant community. It excluded other ant species from the baits in 27 out of 30 cases, and it was excluded only once. No direct interference was observed between *Formica cinerea* and *Myrmica rugulosa*. They coexisted without aggressive interactions on baits.

Discussion

The composition of the Kampinos dune fauna is similar to those found in other successional sandy areas in North and Middle Europe (Boomsma and Van Loon 1982, Gallé 1980, 1986, Járdán *et al.* 1993). The early successional species (*Formica cinerea* and *Lasius psammophilus*) are the same as in the Tvärminne district, Finland (Gallé, 1991), and the similarity between the two total ant faunas is 0.58.

The total densities of ant colonies in the Kampinos study plots are rather low in comparison with other open areas or Polish habitats (Baroni-Urbani and Pisarski 1978, Gallé 1978, 1980, Doncaster 1981, Krzysztofiak 1985, Seifert 1986, Petal and Kusinska 1994). In the Tvärminne dunes, Gallé (1991) found densities between 0.018 and 0.37 nests/m^2. These are surprisingly same as those described in this paper from the Kampinos dunes (also 0.018-0.37 nest/m^2). The average for the different study plots in Tvärminne was slightly lower (0.12 nest/m^2), because more early successional plots with lower densities were sampled in Tvärminne than in Kampinos.

An enormously high density of *Formica cinerea* was found in some early successional study plots (nos. 3 and 7, and other plots in the Kampinos National Park, not involved in this paper), where the densities of this species reached 0.13 colonies/m^2, and the average number of nest entrances was as high as 1.79/m^2. In these sites, the large colonies of *F. cinerea* dominated the whole surface area. Such a high density of F. cinerea was also found in Finland (Gallé 1991 and unpublished). In all these cases, *F. cinerea* was the only or absolutely predominating ant species, without competitors. Under similar conditions, a very high density of *Cataglyphis aenescens* Nyl. was found in the Fülöpháza dune region, Hungary (Gallé, unpublished). The type of the colony pattern represented by F. cinerea is well documented for some *Lasius* species (Brian *et al.* 1966, Levings and Traniello 1981, Traniello and Levings 1986, Gallé 1991, Gallé *et al.* 1993) and it has also been stated that such colony pattern is advantageous, because it reduces the loss of prey (Traniello and Levings 1986) and contributes to the effectivity of food collection of *Lasius* species, which forage both on soil surface and on root aphids (Gunn and Cherrett 1993). Such high density of ant nests and entrances also promotes the infiltration of the soil and probably improve its quality for further successional development (Eldridge 1994, Lobry de Bruyn and Conacher 1994).

The ant species diversities described in this paper are very close to the diversity figures of the ant assemblages in Tvärminne dune area (Gallé 1991). The ant diversity was zero in the first successional stage in Tvärminne, too, and the highest diversity was likewise found in a forest without a high density of red wood ants (2.50 in Tvärminne and 2.19 in the present study). The mean diversities of the transitional stages are also very similar (1.15, 1.86 and 2.26 in Tvärminne, and 1.12, 1.163 and 1.93 in Kampinos, respectively). In both cases, the diversities of ant communities are correlated with those of some structural properties of the habitats (e.g. vegetation architecture). This is in accordance with the results of Withford and Gentry (1981), who also found some relations between the structural heterogeneity of the habitat and the ant community diversity.

The decline of the diversity in the last stage of the studied Kampinos successional series is probably due to the presence of *Formica polyctena,* which is a dominant species in the competitive hierarchy. The top position of this species has been reported by Vepsäläinen and Pisarski (1982), Mabelis (1984), Savolainen and Vepsäläinen (1988), Pisarski and Vepsäläinen (1989) in other areas, too. It was shown by Karlson and Jackson (1981) that the existence of a competitive hierarchy generally decreases the species diversity. In the case of ants, Higashi and Yamauchi (1979), Gallé (1981), Rosengren (1986), Andersen (1992b) and Cammell *et al.* (1996) documented the role of the top species in the reduction of the species diversity. At the same time, we can expect an association between the top competitors and those species that have different life history strategies or body sizes and therefore different niches (cf. Maynard Smith and Brown 1986). Such species are *Leptothorax acervorum* and *L. nylanderi*, which are also typical forest ants in Kampinos, but, since they are very small relative to red wood ants, no competition can be expected between them and *Formica rufa* group species. *Leptothorax* species and *F. polyctena* are correlated in their co-occurrence in Kampinos habitats ($r= 0.63$ and 0.98 $p<0.05$ and <0.001 respectively). In accordance with these findings, Savolainen and Vepsäläinen (1988), also described a close association between *F. polyctena* and *Leptothorax* spp.

The spatial distributions of populations usually reflect the presence or absence of interaction either among the units (e.g. individuals or certain groups of individuals) of the population in question (see Brian 1965, Gallé 1978, 1980, Ryti and Case 1980, 1992, Nielsen 1986, Deslippe and Savolainen 1995, Pontin 1997 for some examples on ants), or between different populations (Shorrocks and Rosewell 1988). No definite trend could be concluded in the present study from the slight differences in the spatial distribution of ant nests between Kampinos habitats, either in the case of single populations, or when all species were considered together. This is in contradiction with the results of the studies in the Tvärminne district (Gallé 1991), where a slight tendency from random towards an arranged distribution was described.

Besides the random spatial colony arrangements, from the low density and co-occurrence rates on both the soil surface and the baits, Gallé (1991) concluded that interspecific interference competition was insignificant in the organization of ant communities in the initial phases of their succession in the Tvärminne dune area. In Kampinos, we have not studied the possibilities of the interspecific competition by observation of the coexistence of foragers on ground surface, but on the basis of low densities we cannot expect high encounter rates and strong interference competition in the early phases of succession. From the data in Table 5, it can be seen that the rate of co-occurrences was low (less than 25 %), even in a site selected for study of the interactions of different populations, which had

Table 5. Statistics of bait experiments

Observations	Species				Total
	F.truncorum	F. cinerea	M.rugulosa	T.caespitum	
No of observations					285
No of positive observations*	97	70	19	6	180
Without coexistence	67	33	7	3	110
Encounters with *F. truncorum*	--	26	2	2	30
Excluded by *F. truncorum*	--	25	1	1	27
Aggression by *F. truncorum*	--	17	1	1	19
Encounters with *F. cinerea*	26	--	10	1	37
Excluded by *F. cinerea*	1	--	0	0	1
Aggression by *F. cinerea*	0	--	1	0	1
Encounters with *M. rugulosa*	2	10	--	0	12
Excluded by *M. rugulosa*	0	0	--	0	0
Encounters with *T. caespitum*	2	1	0	--	3
Excluded by *T. caespitum*	0	0	0	--	0

denser ant populations relative to other successional habitats. It is probable that, at the beginning of the ant community succession, the habitat properties have prior effects on the composition and structure of the ant assemblages (cf. Savolainen and Vepsäläinen 1988).

When co-occurrence was observed, the following hierarchical sequence was found for three species of Tvärminne ants: *Formica sanguinea* (top competitor) - *Lasius psammophilus* (middle-rank species) - *Formica cinerea* (subordinate to both former species). From the results of the bait experiments carried out in this study, it is obvious that *Formica truncorum* is the top competitor among the three species investigated in Kampinos. Both *F. cinerea* and *Myrmica rugulosa* are on the same, subordinated rank. The bottom position of *Myrmica rugulosa* was also shown by Czechowski (1979), who studied the mechanisms of competition between *Lasius niger* and *M. rugulosa*. In the studies that concern the competitive hierarchy of ant species (e.g. Pisarski 1978, Czechowski 1979, DeVroey 1979, Reznikova 1980, Vepsäläinen and Pisarski 1982, Mabelis 1984, Haering and Fox 1987, Czechowski and Pisarski 1988, Andersen and Patel 1994), the interference competition is emphasized, and in some publications even the life history strategies of ant species are classified on the basis of their relation to the top competitors (see Andersen 1986a). In the present study, the existence of an interference competition is obvious in the relation of red wood ants (*Formica polyctena* and *F. truncorum*) to other species. For the *Formica cinerea* - *Myrmica rugulosa* species pair, only a possibility of exploitation competition can be concluded from the absence of direct interactions on baits.

It is predicted that larger species are more successful in the interference competition (Persson 1985). This prediction accords with our present results on the relation between red wood ants and other species, but in some species pairs (e.g. *Formica cinerea* and *Lasius psammophilus* in Tvärminne; Gallé 1991) the larger species are subordinated because of their avoidance behaviour on baits (see also Fellers 1987). It is also a general opinion that the scarcity of resources promotes interference competition (Schoener 1982). On this basis we should expect the most intensive interference in the very early successional stages (e.g. plots 1, 2, 3, and 5), with the lowest food supply. However, since the density of forager ant workers and their encounter rates are low, in such places, the different ant populations can effect each other's success mainly by influencing their common prey (see also Gallé 1991), i.e. by exploitation competition.

The vegetation architecture, the number and condition of the dead twigs on the ground surface and the composition of the epigeic invertebrate fauna are assumed to be of importance in differentiating the composition of ant communities in this study. The same habitat properties were found to be probably effective in the Tvärminne district (Gallé 1991). In sand dune areas of southern regions in Hungary and Turkey, however, under more extreme climatic conditions, the microclimate was also correlated with ant community composition (Járdán *et al.* 1993, Gallé unpublished). Both the architecture of the vegetation and the number and condition of the twigs are important components of habitat complexity and heterogeneity. The influence of the vegetation architecture and/or habitat structural heterogeneity on the composition of ant communities is well known and has been discussed by several authors (Culver 1974, Room 1975, Withford and Gentry 1981, Andersen 1983, 1986a, Majer *et al.* 1984, Gallé 1991, Bestelmeyer and Wiens 1996). The main effects of the vegetation architecture are probably indirect through modification of the microclimate, the influence on nesting sites and

determination of the food supply (see also Andersen 1986a), but there might also be direct effects, e.g. during the habitat selection of fertilized females.

Acknowledgment

The publication of this study was supported by the Hungarian Scientific Research Fund OTKA No T 020149. The authors thank the Department of Zoology, Polish Academy of Sciences and Lomna Zoological Station for working facilities. We remember especially gratefully late Professor Bohdan Pisarski, who helped a lot in the organization of our study and reviewed our manuscript. We thank an anonymous referee for the review of a former draft of this paper. Special thanks are due to Gabriella Szőnyi for her manifold help in preparing the manuscript.

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TISCIA 31, 29-33

„OUTLAWS": SOME EVOLUTIONARY ASPECTS OF RARITY IN INSECTS

L. Papp

Papp, L. (1998): „Outlaws": some evolutionary aspects of rarity in insects. — *Tiscia 31, 29-33.*

Disorder is limited; the only question is the size of its box (I)

Abstract. The term „rare" must always have a practical and operative meaning. The discussion is introduced by consideration of some trivialities: 1) potential and actual population sizes are as important properties of an evolving species as any morphological, physiological or other features; 2) every species is rare at rise; 3) most insect species are rare. The importance of distinguishing the ecological and the evolutionary meaning of rarity is stressed. Their incongruence is a consequence of a number of reasons, e.g. there is no direct correlation between local rarity and the niche dimensions, the mean size of populations and the size of distribution area, etc.
Speciation (of an abundant species) is a process of maturation. In *statu nascendi* every new species is isolated (and exists in low numbers), but having left isolation its potentials and constraints (competitive, predator-prey, etc. relationships with the extant species) will determine further steps of speciation. From this viewpoint rare species are premature species: they have never reached the phase (population size) of confrontation (competition, etc.). However, under the umbrella of abundant species, rare species are released from most community constraints and hence they are objects in the laboratory of Nature: „hopeful monsters" are possibly derivatives of rare species.

Key words: evolution, speciation, population size, rarity.

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The notion of „rarity" has become rather popular in ecology. This is a recent development, though. It was only four years ago when the first modern book on rarity as such was published. The significance of Gaston's (1994) work cannot be overestimated, I am certain.

The first question, as it is always so — what is rarity. (I think it would be disadvantageous to base any further discussion on the difference in the meaning of „rare" and „scarce", obviously existing in English). What I think of this term is that we must not think of a clear and clear-cut notion if we mention rarity. This is very much of a weak, relative (comparative) notion, though it seems important for various reasons. No wonder that there is much confusion about the meaning of „rare".

Although there are theoretical problems with rare species, the delimitation of the term „rare" must always be very practical and operative. This is why I would propose a cut-off point of 1 %, 0.5 % or 0.1 % of species frequency in a given sample, or, 1 %, 0.5 % or 0.1 % of the frequency of the dominant species in the sample; depending of the aims of the study and on the taxonomic group under study. Much to my regret, I have to say that Gaston's otherwise very good book has not made things stand better at all. He suggested „that a useful cut-off point is the first quartile of the frequency distribution of species abundances or range sizes" (i.e. a cut-off of 25 %).

I am not going to discuss all the controversial consequences of such a cut-off, and I do not want to provoke a debate on criteria of rarity: a practical term is under the permanent test of the practice. I would rather show an example from my works, a frequency distribution of a given sample of flies on elephant dung in Africa (Fig. 1). The 49 dipterous species (a total of 3 677 specimens) are ranked from the commonest to rarest, frequencies being given on a logarithmic scale. The two horizontal lines are at the 1 % and 0.1 % level of the relative frequency; the

dotted line is at the 1 % level of the dominant species. The vertical line is Gaston's cut-off of the first/last quartile, which results in some of the species represented by singletons being regarded as *not rare*!

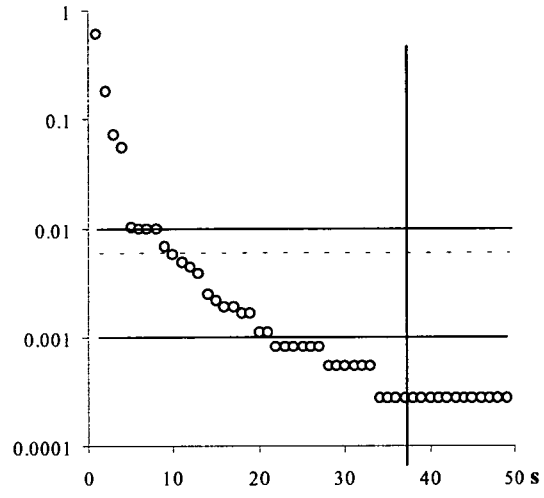

Fig. 1. Frequency distribution in a sample of dipterous species observed on elephant dung in Tanzania (relative frequencies of 49 species, logarithmic scale; s: serial number of species in frequency; explanation in text)

Gaston's argumentation for his definition is weak, I think, but otherwise his book is of an historically important scientific value. (An interpretation of the frequencies from common to rare as a continuum does not hinder but rather facilitates studies on the causes of rarity. On the other hand, it is true that it is always the researcher who must decide on the level of rarity, but I think this necessity of decision as unavoidable).

I believe, D. Rabinowitz's (1981) paper on the seven forms of rarity is a mile-stone in the scientific approach to rarity. Since her works are so well-known, I do not repeat their summarizing table here (with examples of flowering plants in order to remind you the „three traits" etc.). I can only admit that the eighth box is not empty for flies, though the rare species are not inclined to be specialists, or at least they are not exclusively so. If we conceive those three traits as three continua (and modify local population size „somewhere large" to „large"), we obtain a three-dimensional space or rather a cube; let me call that cube „DebRa's cube". It is easy to understand that there is only one negative apex on that cube, where all the three traits have their maxima (globally thinking; of course, negative for rarity). And it is easy again to realize that not only the other apices, but an infinite number of other points on the sides of the cube and inside the cube may represent rare species. It is useless to say that one can find also other traits for similar consideration.

There has been much confusion about the interpretation of rarity. This is why I think Gaston's book is so important. I do not want to discuss those misinterpretations in details, only I must mention Hanski's core-and-satellite species model (Hanski 1982, for some other respects see Nee *et al.* 1991), which was misinterpreted for the rare-and-abundant continuum, very much against the original aims of its author.

In my opinion the main cause of the confusion is a lack of distinction of the ecological and evolutionary meaning of rarity. I emphasize the importance of such a distinction. The incongruence of the ecological and the evolutionary meaning of rarity is a consequence of a number of reasons, e.g. there is no direct correlation between local rarity and the niche dimensions, mean size of the populations and the size range of distribution, just to refer to DebRa's cube. Consequently, my definitions are:

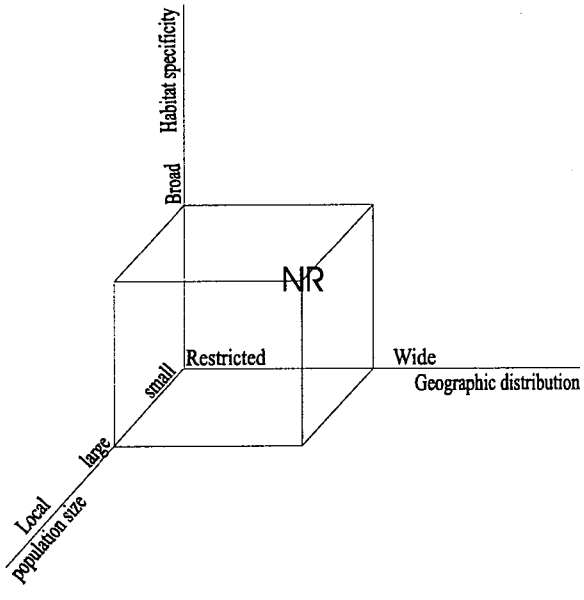

Fig. 2. From the „Seven forms of rarity" to DebRa's cube: to illustrate that an immense number of forms or rarity exists (cf. Rabinowitz *et al.* 1986).

The ecological meaning of „rarity" is no more than a low relative frequency in the samples as a consequence of any cause. The level of cut-off is always determined by the researcher based on practical criteria.

The evolutionary meaning of rarity is that the species is extant globally in low numbers (population

size in any context of population biology is better interpretable as effective population size). The two kinds of meaning are rarely congruent and it is so for species just before their extinction. Paraphrazing the title of Rosenzweig's (1995) excellent book, we may speak about „rarity in space and time".

Considering the above reasons, rarity needs to be interpreted for every species and in every actual case, since it is interpretable *only in concrete cases.* For such an interpretation we must have sufficient information on the bionomics, phenology and other traits of the given species.

If there is so little to be generalized about the „rare" species, is there any reason to seek for general considerations about their phylogeny? Well, in the meagre discussion below I would rather stress some *common ecological features of the rare insects, which may have evolutionary relevances.*

As regards rarity in insects, the starting point of the discussion is a consideration of some trivialities: 1) the potential and actual population sizes are just as important properties of an evolving species like any morphological, physiological, etc. features; 2) the majority of the insect species are rare; 3) every species is rare at rise. One may say that the third point is not always true; that is, there are evolutionary situations when the transformation of the species occurs in large populations. I am aware of that but those cases are not the topic of the present paper.

As for the evolutionary factors affecting gene frequencies in rare species, of course mutations and meiotic drift must have the same role as in the abundant species. *Migration is important in those species only* that *exploit permanent resources, since dispersal for new evanescent resources (like small dead animals, fresh dung etc.) makes consideration of migration in the usual sense inoperative.* As McKinney *et al.* (1996) showed generally and convincingly „rare species having a patchier (less uniform) distribution in both time and space".

Actually I think that genetic drift plays the most important role in their speciation by producing *extremely fit* populations by chance. The probability of such an event is very low, but the number of the possible cases is high. The main role of selection is to maintain the fittest ones, as always so.

The ecologically interpretable general traits of the rare species are as follows:

Quite contrary to the abundant species, where predation by *definite* predatory populations, or parasitism by more or less specialised parasites are major factors in control of population size, the majority of the specimens of rare species are lost in the course of their quest for finding „new" resources; and *if it is so, their main limiting factors are out of the community they belong* (in other words, for a high number of rare species: minute sources, very large sinks, cf. Pulliam (1988)). Therefore the stochastic processes in dispersal are far more important for them than even a strong selective pressure *at some given points* of their range. On the other hand, such kind of a rare species must have good potentials of spreading and strong bases in its recognition system. So most of what is said in this paper applies to flying insects only.

They are not involved in competitive processes at all. I would call them „outlaws", since — with some exaggeration I would say — they are under a single community constraint only: they must not exceed a given level of abundance. Their local extinction and local recolonisation are not only common processes but *this is their way of existence.* It is useless to say, all these cause a lot of problems when we want to determine their range of distribution etc.

It is well-known that rare species form the majority, not only within a given guild, but even within the taxonomic groups. This phenomenon is known under various „laws" in ecology, like Monard's law, Monard-Balogh's law, namely, there is only a single abundant species from every genus in a community and most of the species in a genus are rare (Papp 1993). And just the populations of the abundant species *with similar ecological traits, with the same predators and parasites form an umbrella over the rare ones.* They are predated and parasitized in proportion to their relative frequencies, which results in the outlaw — in some respects a constraintless — position of the rare species (cf. eg., Lawton 1984). It is incorrect to think of the rare insect parasitoids as parasitoids of rare species. That would be too costly.

The speciation processes which produce rare species from rare species are common and take place easily, but they are mostly negligible for the main directions of global macroevolution. From our viewpoint those evolutionary situations are interesting when a rare species becomes abundant, or when an abundant species gives birth to numerous rare ones.

Of course, there must have been cases in the evolutionary history of insects when a rare species became abundant. However, an abundant species has to be fit in competitive, predatory, and other interactions. We have to acknowledge that numerous species or even the majority of the species do not accept the challenge and hence they remain rare.

Speciation (of an abundant species) is a process of maturation. *In statu nascendi* every new species is

isolated in the physical or in the ecological space (and exists in low numbers), but having left isolation its potentials and its constraints (competitive, predator-prey and other relationships with the extant species) will determine the further steps of speciation. From this viewpoint the rare species are premature species: they have never reached the phase (population size) of confrontation (competition with other species etc.). However, under the umbrella of abundant species, rare species are released from most community constraints and hence they are objects in the laboratory of Nature: the „hopeful monsters" are derivatives of rare species. Indeed, Nature's „extension laboratory" works at least partly on the principle of trial-and-error. Or if that is a game, this game is played by high number of players and with very high number of cards (so there is a chance for a royal flush for some).

I can stress again that the main directions of macroevolution are markedly determined by the abundant species, but „hopeful monsters" are more likely to evolve from rare ones. Rarity is a proper condition for endeavours. Among those circumstances the efforts are not limited by competition and are rather little constrained by predation and parasitism.

Although it is not always so, it must be a common phenomenon that the evolving „new" species exist in low numbers, even if they are derivatives of an abundant one, or even if later they become abundant. Several isolated populations of a widespread and abundant species can transform into separate species within a given period. Since an abundant species has a better chance to produce a new branch within a given period than a rare one, branches that include abundant species are less likely bifurcating; their multifurcation must be far more frequent than those of the rare species. An assumption of multifurcations in several heleomyzid genera (Diptera) during the Ice Ages is surely a better hypothesis than bifurcations exclusively.

In the case when several rare species are formed from an abundant one consecutively, or the alternative case, where the present day abundant species has an intermediate position among rare ones (in this case some important change must have happened sometime in that evolutionary period), are analysed in a subsequent paper.

I must stress that I do not want to pose a new hypothesis here but *a new simple test in the evolutionary analysis,* however, it needs better elaboration.

As it may be seen on Rabinowitz's table, species with wide geographic distribution, broad habitat specificity and somewhere large local population size may be found rare locally (for instance at the edge of its distribution, in habitats representing extreme values of its niche, etc.). Again, an infrequent question among the problems of low abundances is that species which are able to live in abundant numbers, may also occur and live in a number of other communities *at low frequencies.* (A well-known example is the occurrence of the house fly in pastures of Central Europe: it is extremely rare there). I think this is an important component of their evolutionary strategy. In those „alien" communities populations of other species form the umbrella above them. In several communities there is a „shift system" among the species that are able to exist as abundant. This is an important balance to yearly, seasonal or other changes of environmental factors by which the community is capable to react dynamically. An example is given in Table 1, where the frequencies of agromyzid species in cereal fields of Hungary are shown in three consecutive years.

Recall that the neodarwinian synthesis had considerations of the abundances (actually the population sizes), though I think the different population sizes have not been properly analysed from the viewpoints of speciation. Cladistic theory does not and *cannot* take the different frequencies of the species into consideration. This is one of its weakest points. (Some consequences to cladistics are discussed in a forthcoming paper.)

Table 1. Percentile frequencies of agromyzid species in cereals in three consecutive years in Hungary (100 net sweeps/sample, on the average five samples per county; from Papp 1993)

species	1987	1988	1989
Agromyza intermittens	0.11	1.75	1.51
luteitarsis	58.71	1.57	1.62
megalopsis	0.83	8.89	1.57
nigrella	9.07	85.43	93.68
nigrociliata	2.31	0.96	0.25
rondensis	28.40	0	0.09
Phytomyza fuscula	0.22	0.68	0.85
other species	(4 spp.)	(5 spp.)	(9 spp.)
% combined	0.35	0.72	0.43
total number of individuals	2768	2801	8953
total number of samples	63	46	57

In summary, the present paper is aimed at a discussion of the basic concept of „rarity" in evolutionary studies and to serve as „food for thought" for a better approach.

The problems in generalisation of the meaning of „rarity", the extremely high diversity in life habits, life history strategy and other evolutionary biological features of the rare insect species make it difficult to establish laws of wide validity in the evolutionary aspects of rare species (or even to risk statements of generalization). What we really know by now is that „big" ecological invariance principles, the general models in population biology and the

prevailing theories of speciation are hardly valid for them. This statement will not mean that prevailing theories (and models) are actually to be revised. *All those theories are valid for the abundant species which control the main biotic processes on Earth, the matter and energy flows and biotic constraints.* On the other hand, the generalizations for all the species are surely invalid.

The majority of the species on Earth (at least so for the insects) are rare and insignificant as for the ecological processes. Nevertheless when one investigates the revolutionary changes in macro-evolution, one must more frequently think of the rare species, the outlaws, the chips of macroevolution. Or simply but more generally, if we are really concerned about the knowledge of biodiversity on Earth (I mean its quality, quantity and its evolution), they must not be neglected.

Acknowledgements

The main points of this paper were involved in an oral presentation at the ICSEB V (Budapest, 17-23 August 1996). The first version of this paper was submitted to Acta zool. hung., but finally refused. I would like to thank for all the (eight) readers for their criticism, although some of them were obviously unable to get rid of preconceptions. Some claimed detailed treatment of the prevailing ideas, etc. However, I am to publish a short paper only and not a book, where I deal with less questions than in the original version in order to form a message more effectively.

I am grateful to Dr. András Demeter for improving the English of the manuscript and for his useful comments.

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TISCIA 31, 35-39

LIFE FORM SPECTRA OF ORTHOPTERA FAUNA IN ALKALINE GRASSLANDS

I. A. Rácz

Rácz, I.A. (1998): Life form spectra of Orthoptera fauna in alkaline grasslands. - *Tiscia 31, 35-39.*

Abstract. The reasons for the attachment of Orthoptera communities to grasslands have not been revealed yet. We can assume that similar plant associations - because of the species compositions - have similar structure, thus rather similar microclimatic conditions as well. Thus, the spreading of some species - mainly stenoc species - corresponds with the spreading of the given plant community in a great extent, so the given plant association groups have their characteristic Orthoptera groups with their species combination. Besides the quantitative analysis of these, there is a need to analyse the qualitative parameters as well, since the members of eco-faunas organized within the given habitat can be ranked among different life form types, so the given plant communities can be characterized not only on the basis of their Orthoptera group compositions, but with the ratio of life form types dependent on the plant structure.
In the present work we analysed data collected with quantitative methods from 10 sampling sites, which represents our alkaline grasslands - 3 from Kiskunság, 7 from Hortobágy. The aim of our research is to analyse the connection between the different grassland structure and the given life form types. Our results indicate, that the different alkaline grasslands - depending on their structure - can be characterized by the life form spectrum of the Orthoptera communities.
This calls our attention from the point of view of conservation and cultivation as well to fact, that disturbances which change the structure of the grasslands can extremely influence the composition of the given Orthoptera fauna, even cease the conditions of existence for some species.

Keywords: grassland structure, life form spectrum, life form types, Orthoptera communities.

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Introduction

Although the fact that the Orthoptera communities are highly connected to grassland communities (Rácz *et al.* 1994), the reasons for this are less known. We might assume, that similar plant associations - because of their species compositions - have similar structure, thus rather similar microclimatic conditions as well. Thus, the spreading of some species - mainly stenoc species - corresponds with the spreading of the given plant community in a great extent, so the given plant association groups have their characteristic Orthoptera groups with their special species combination (Nagy 1944, Rácz and Varga 1978, Varga and Rácz 1986, Rácz 1986, Vargáné Sipos *et al.* 1994).

With the quantitative analysis of these - qualitative and quantitative species composition analysis - the changes in the given associations can be well traced, however besides this there is a need to analyse the qualitative parameters as well, since the members of species-groups organized within the given habitat can be ranked among different life form types (Nagy 1944, 1947, Bei-Bienko 1950, Pravdin 1978, Stolyarov 1976, Stebaev and Nikitina 1976), so the given plant associations can be described not only by the characteristic composition of their Orthoptera groups, but with the ratio of life form types (Rácz and Varga 1996a, 1996b, Rácz 1997), which depends on the plant structure (Dorda 1998).

The aim of our research was to analyse the connection between the structure of different grasslands and the life form types of the connected Orthoptera groups, and to answer the question whether grasslands with different structures can be

characterized by the life form spectrum of the Orthoptera communities.

Materials and Methods

In the present work we analysed data collected with quantitative methods from 10 sampling sites. The sites represent the most important alkaline grasslands of Hungary (3 sampling sites in Kiskunság (Rácz 1986), 7 in Hortobágy) (Table 1).

To determine the life form types we used the types of Bei-Bienko, modified by Pravdin (Bei-Bienko 1950, Pravdin 1978), and our field experiences.

Using the group-dominance values of the given sampling sites' Orthoptera groups we examined on one hand the life form spectrum of the given samples, and on the other hand we calculated quantitative distance value among the samples and the data matrix obtained was analysed by multivariable statistics (Nucosa 1.05: Czekanovsky index, cluster analysis, principal component analysis, Tóthmérész 1993).

Results

On the basis of the types of Bei-Bienko and our field experiences we could determine 7 life form types. These are the followings: thamnobiont, chortobiont, and geobiont, which can be separated on the basis of morpho-ecological and behaviour-ecological parameters, and the chorto-thamnobiont, chorto-geobiont, geo-chortobiont, geo-psammobiont life forms, which can be separated on the basis of their behaviour-ecological features.

Analysing the relative frequency distribution of the life form groups of different Orthoptera taxa we can state the following general findings:

From the results of the multivariate analyses we can conclude, that there is a clear separation among the Orthoptera taxa of the grasslands examined according toh their life form spectrum. The following samples form distinct groups (Fig. 1), which can be confirmed by the results of cluster analysis as well (Fig. 2): 1, 2, 5, 8, 9, 10, 11 and 3, 4, 6, 7.

The first main group (I) consists of associations of humid, almost or completely closed, well-structured loess and alkaline grasslands, with high (more than 40%) dominance of chortobionts, in two groups.

The associations of the group I/1 - (1, 2, 5, and 9; *Salvio-Festucetum, Peucedano-Asteretum, Agrosti-Alopecuretum, Agrosti-Caricetum*, respectively) which can be characterized by the high dominance of chortobionts and the lower dividend of geo-chortobionts - represent the closed, well-structured grasslands that contain undergrowth grasses. This type is indicated by the chorto-thamno- and thamnobiont life form types.

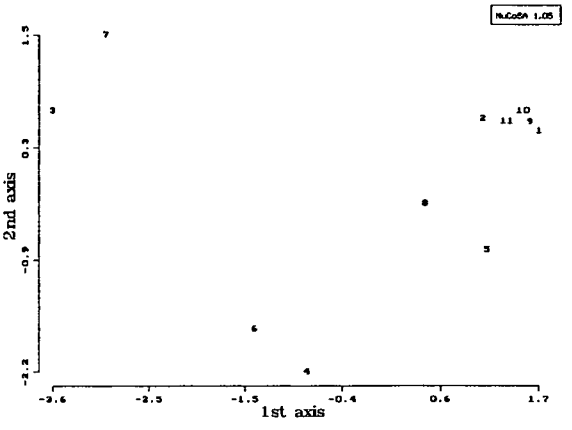

Fig. 1. Principal component analysis of sampling sites

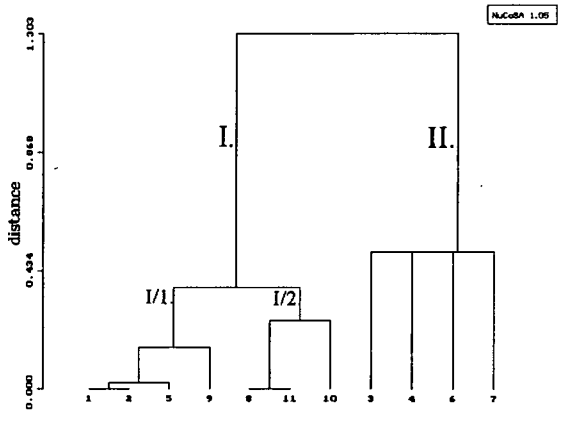

Fig. 2. Cluster analysis of sampling sites

The group I/2 is formed by the grasslands 8, 11, 10; *Suaedetum* and the typical and mosaic *Artemisio-Festucetum*, in which the chortobiont species are dominant. The lower covering values are indicated by the higher presence rate of geo-chortobiont life form type.

The second main group (II) is formed by the xerofil, usually - in some extent -open grass associations (3, 4, 6, 7; *Achilleo-Festucetum, Artemisio-Festucetum, Puccinellietum, Camphorosmetum*, respectively) with the significant dominance of geo-chortobiont life form. The geobiont life form indicates the plant shortages, however with relatively low values.

Table 1. The Orthoptera species of plant communities

		Hortobágy								Kiskunság		
		1	2	3	4	5	6	7	8	9	10	11
Life forms	Species / Plant-communities	Salv.-Fest.	Peuc.-Aster.	Achill.-Fest.	Art.-Fest.	Agro.-Alop.	Pucci.	Camph.	Suaede-tum.	Agr.-Car.	Art.-Fest.	Art.-Fest.
ch	Paltycleis grisea	0.002	0.008	0	0	0	0	0	0	0	0	0
ch	Platycleis affinis	0.011	0	0.028	0.001	0	0.002	0	0	0	0.021	0.052
ch	Tesselana vittata	0.064	0.005	0.006	0.001	0	0	0	0	0	0.000	0.000
ch	Bicolorana bicolor	0.0004	0.008	0	0	0.003	0	0	0	0	0	0.010
ch	Roeseliana roeselii	0.005	0	0	0.001	0.017	0.002	0	0	0.015	0	0
ch	Parapleurus alliaceus	0.001	0.002	0	0	0	0	0	0	0.091	0	0
ch	Chrysochraon dispar	0	0.002	0	0	0	0	0	0	0.015	0	0
ch	Euthystira brachyptera	0	0.000	0	0	0	0	0	0	0.015	0	0
ch	Stenobothrus nigromaculatus	0.004	0.002	0.014	0.001	0	0	0	0	0	0	0
ch	Omocestus ventralis	0.102	0.204	0.047	0.017	0.010	0.020	0.051	0	0	0.021	0.073
ch	Glyptobothrus mollis	0.003	0.007	0	0	0	0	0	0	0	0	0
ch	Chorthippus albomarginatus	0.113	0.081	0.105	0.055	0.615	0.223	0	0.379	0.076	0.536	0.151
ch	Chorthippus dorsatus	0.036	0.071	0.044	0.002	0.048	0.008	0	0.034	0.030	0.05	0.016
ch	Chorthippus loratus	0.002	0	0.001	0.001	0.017	0.001	0	0	0	0	0
ch	Chorthippus dichrous	0.044	0	0.006	0.005	0.038	0	0.026	0	0.030	0	0
ch	Chorthippus parallelus	0.113	0.081	0.112	0.008	0	0.072	0	0	0.318	0.014	0.115
ch	Chorthippus montanus	0	0.005	0.001	0	0	0	0	0	0.061	0	0.016
ch	Tetrix subulata	0.0004	0.002	0	0	0	0.001	0	0	0	0	0
ch	Tetratetrix bipunctata	0	0.013	0	0	0	0	0	0	0	0	0
ch	Tetratetrix nutans	0.001	0.005	0.001	0	0	0	0	0	0	0	0
ch-g	Acrida hungarica	0.006	0.002	0	0	0	0	0	0	0	0	0
ch-g	Stenobothrus crassipes	0.052	0.156	0.013	0.005	0.007	0.028	0	0	0	0	0.042
ch-g	Stenobothrus stigmaticus	0.001	0.002	0.002	0.073	0	0.001	0	0	0	0	0
ch-g	Glyptobothrus biguttulus	0.016	0.003	0	0	0	0	0	0	0	0	0
ch-g	Glyptobothrus brunneus	0.060	0.005	0.028	0.005	0	0.013	0	0	0	0.007	0.016
ch-g	Dociostaurus maroccanus	0	0	0	0.001	0	0	0	0	0	0	0
ch-g	Dociostaurus brevicollis	0.022	0.002	0.087	0	0	0.244	0	0	0.136	0.021	0.063
ch-th	Decticus verrucivorus	0.002	0	0	0	0	0	0	0	0.030	0	0
ch-th	Gampsocleis glabra	0.010	0	0.003	0	0.017	0	0	0	0.030	0	0
g	Oedaleus decorus	0	0	0	0.002	0	0	0	0	0	0	0
g	Celes variabilis	0	0	0	0.022	0	0	0	0	0	0	0
g	Oedipoda coerulescens	0	0	0.009	0.015	0	0.002	0.128	0	0	0	0
g-ch	Calliptamus italicus	0.003	0	0.004	0	0	0	0	0	0.152	0	0
g-ch	Aiolopus thalassinus	0.002	0.028	0.011	0.021	0	0.020	0.154	0.276	0	0.164	0.021
g-ch	Epacromius coerulipes	0	0.005	0.012	0.026	0	0.153	0.179	0.276	0	0	0
g-ch	Dirschius haemorrhoidalis	0.044	0	0.149	0.064	0.027	0.039	0.026	0.034	0	0	0.010
g-ch	Dirschius petraeus	0	0	0.081	0.390	0	0.106	0.385	0	0	0	0.005
g-ch	Euchorthippus declivus	0.259	0.267	0.226	0.032	0.131	0.049	0.051	0	0	0.029	0.380
g-ch	Euchorthippus pulvinatus	0.001	0	0	0	0	0	0	0	0	0	0
g-ch	Myrmeleotettix maculatus	0.0004	0	0	0	0	0	0	0	0	0	0
th	Meconema thalassinum	0	0.002	0	0	0	0	0	0	0	0	0
th	Conocephalus discolor	0.001	0.032	0.006	0	0.041	0.008	0	0	0	0.007	0.026
th	Conocephalus dorsalis	0.002	0	0.001	0	0.027	0.002	0	0	0	0.064	0
th	Homorocoryphus nitidulus	0.0004	0	0	0	0	0	0	0	0	0.064	0
th	Tettigonia viridissima	0.001	0	0	0	0	0	0	0	0	0	0.005
th	Oecanthus pellucens	0.016	0.002	0.001	0	0	0	0	0	0	0	0
	No. of species	35	27	28	23	13	22	8	5	13	12	16

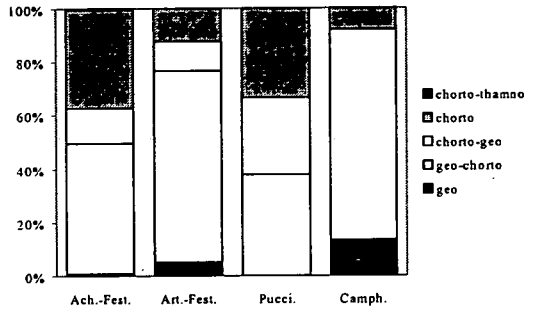

Fig. 3. Life form spectra of plant communities (main group I)

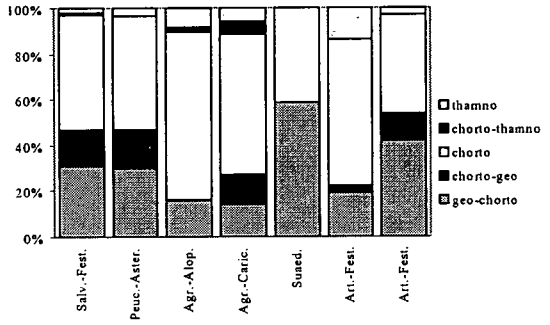

Fig. 4. Life form spectra of plant communities (main group II)

Discussion

It is clear, that the Orthoptera group of the *Peucedano-Asteretum* association shows the life form distribution characterizing the loess grasslands, and not the alkaline grasslands, that is, the chorto- and thamnobiont species are dominant with the characteristic Tettigonoidae (*Conocephalus discolor, Platycleis grisea, Tesselana vittata, Bicolorana bicolor, Gampsocleis glabra*), while the subdominant chorto-geobionts are the Acridoidae (*Stenobothrus crassipes, Glyptobothrus biguttulus* and *brunneus*).

The species compositions of the Orthoptera groups of the dry grasses of the better quality alkaline grasslands (Hortobágy, Kiskunság) can be regarded as the poorer version of loess grasslands. This manifests in their life form spectrum as well, since mainly the chorto-and geochortobiont groups are dominant (species of *Chorthippus, Glyptobothrus* and *Dirschius* genera), while the chorto-thamnobiont life form is subdominant (*Decticus verrucivorus, Gampsocleis glabra*).

In the semi-desert-type associations with short grasses the geo-chortobiont dominance is unambiguous (*Epacromius coerulipes, Aiolopus thalasinus*), and depending on the degree of the openness, geobiont species like *Oedipoda caerulescens*, *Calliptamus italicus* and *Celes variabilis* appear as well. However, we can clearly state, that these species groups are also poor in Tettigonoidae, similarly to the sandy grasslands.

From the above, the different dry and semi-dry grasslands can be clearly characterized by different Orthoptera life form distribution which depends on the degree of covering and levels. Open associations can be described by high geo- and geochortobiont dominance, while in the fairly closed grasses the chorto-geobionts are dominant, and in the closed grasses the chortoboints. In grasses which have more layered structures, however, besides the dominance of the chorto-geo- and chortobionts, the less closed ones are characterized by the geo-chortobionts, while the closed, well-structured ones are characterized by the chorto-thamno and thamnobiont life forms.

So, we can conclude that the given grasslands can be described not only by the quantitative features and the species compositions of the connected Orthoptera groups, but - depending on their structure - by their life form spectra as well. This also calls our attention to the fact which is important from the point of view of conservation and cultivation as well, that all disturbances (like cancellation of mowing, in appropriate grazing, afforestation) which can change the structure of the grasslands can extremely influence the quantitative and qualitative composition of the given Orthoptera fauna. In extreme case, by ceasing the conditions of existence for some species it can cause the extinction of them.

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TISCIA 31, 41-45

TISZABERCEL BIOMONITORING PILOT PROJECT — QUANTITATIVE ORTHOPTEROLOGICAL RESEARCH

I. A. Rácz

Rácz, I.A. (1998): Tiszabercel Biomonitoring Pilot Project — Quantitative Orthopterological Research. - *Tiscia 31, 41-45.*

Abstract. Our results prove, that grasslands in different succession state or influenced by human activities, on the flooded area were suitable as sampling sites. In contrary to the disturbances, we found a fairly rich (25 % of the Hungarian fauna) and diverse orthoptera community on the area. In the fresh, very humid grasslands the ratio of the predator Tettigonoida is high, in which the definitely thamnobiont-hygrophilous species are characteristic (*Conocephalus, Ruspolia*). Also the species of the characteristic chortobiont Acridoidea of these associations (*Chrysochraon, Parapleurus* and *Mecosthetus*) are strongly hygrophilous. With the decreasing humidity, and as the grassland structure becomes simpler, these species disappear, and those Acridoidea become dominant, which need at least seasonal hygrophilous environment at the early stage of their onthogenesis. On the other hand, it is very typical the significant difference between the Orthoptera fauna of the less and the highly disturbed grasslands. The heavily grazed or intensively cultivated grassland's Orthoptera species composition is quite poor, or can be characterized by one or two ubiquist species. This fact also call our attention to that the strong disturbance can extremely change the composition of the Orthoptera fauna.
Thus, this insect group is highly important not only from the point of view of fauna- and florahistory, but community- and productionbiology, that is indirectly economic and conservational point of view as well. Regarding the bioindicator value of this group, we can conclude, that using either the theory of physiological tolerance, or the theory of community answer as a starting point they are suitable for indication. Since, if we study the qualitative changes of the species composition, or the distribution of the high diversity frequency, we can point out the significant changes of features of the given area.

Keywords: diversity, monitoring, orthoptera, perturbancy, quantitative analysis.

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Introduction

The monitoring project is dealing with a comparative study of grasslands of different associations, conditions and cultivation on the inundation area of both sides of Tisza river, and aims to answer the questions related to the conservation (treatment) management and the use of these areas.

Material and methods

The sampling sites located both on the inundation area (5 samples: 1, 2, 3, 4, and 8) and on the protected side (6 samples: 5, 6, and 7, 9, 10, 11) in grasslands of different associations and conditions (Table 1).

Table 1. Sampling sites of inundation area and protected side

Inundation area	Protected side	Inundation area	Protected side
1. Diófa-lapos (Gávavencsellő)	5a. Lenc (Gávavencsellő)	7. Remete-zug (Gávavencsellő)	8. Görbe-tó (Balsa)
2. Mocsolya (Gávavencsellő)	5b. Lenc (Gávavencsellő)		9. Görbe-tó (Gávavencsellő)
3. Lomos (Gávavencsellő)	6. Gyuj-tava (Gávavencsellő)		10. Pók-tava (Tiszabercel)
4. János-tó (Gávavencsellő)			11. Füzes-ér (Tiszabercel)

Table 2. List of species

Taxon	Geographical range	Faunal type	Life forms	Relative ab.	Cat.
Ordo: Ensifera (Grylloptera)					
Phaneroptera falcata (Poda 1761)	Eu-Si	Si-Pc	Th	0.252	IV
Leptophyes albovittata (Kollar 1833)	Eu	Po-Med	Th	0.188	III
Conocephalus discolor Thunberg 1815	Eu-Si	Si-Pc	Th	0.335	IV
Conocephalus dorsalis (Latreille 1804)	Eu-W-As	Po-Ca	Th	0.111	II
Ruspolia nitidula (Scopoli 1786)	Af-Eu-Si	Af	Th	0.095	II
Tettigonia viridissima Linne 1758	Eu-Si	Si-Pc	Th	0.169	III
Decticus verrucivorus Linne 1785	Eu-Si	An	Ch-Th	0.21	III
Platycleis affinis Fieber 1853	SE-Eu	Po-Ca	Th	0.143	III
Bicolorana bicolor (Philippi 1830)	Eu-Si	An	Ch	0.159	III
Roeseliana roeselii (Hagenbach 1822)	Eu	Po-Ca	Ch	0.22	III
Gryllus campestris Linne 1758	Af-Eu-W-As	Af	Fi	0.124	II
Ordo: Caelifera (Orthoptera s.str.)					
Calliptamus italicus (Linne 1758)	Eu-Si	An	Geo-Ch	0.178	III
Mecosthetus grossus (Linne 1758)	Eu-Si	Ma	Ch	0.191	III
Parapleurus alliaceus (Germar 1817)	Eu-Si	Ma	Ch	0.099	II
Chrysochraon dispar (Germar 1834)	Eu-Si	An	Ch	0.105	II
Euthystria brachyptera (Ocskay 1826)	Eu-Si	An	Ch	0.121	II
Stenobothrus crassipes (Charpentier 1825)	E-Eu	Po-Med	Ch	0.201	III
Omocestus ventralis (Zetterstedt 1821)	Eu-Si	An	Ch	0.313	IV
Omocestus haemorrhoidalis (Charpentier 1825)	Eu-Si	An	Ch	0.293	IV
Glyptobothrus biguttulus (Linne 1758)	Eu	Po-Ca	Ch	0.434	IV
Glyptobothrus brunneus (Thunberg 1815)	Eu-Si	An	Ch	0.523	V
Glyptobothrus mollis (Charpentier 1825)	Eu-Si	An	Ch	0.351	IV
Chorthippus alobomarginatus (DeGeer 1773)	Eu-Si	Si-Pc	Ch	0.306	IV
Chorthippus dorsatus (Zetterstedt 1821)	Eu-Si	Si-Pc	Ch	0.46	IV
Chorthippus parallelus Zetterstedt 1821	Eu-Si	An	Ch	0.399	IV
Euchorthippus declivus (Brisout 1848)	S-Eu	N-Med-Pc	Geo-Ch	0.402	IV
Dociostaurus brevicollis (Eversmann 1848)	Eu-Am	Po-Ca-Tur	Geo-Ch	0.162	III
Tetrix subulata (Linne 1758)	Ho	Eu-Pc	Ch	0.188	III
Tetratetrix bipunctata (Linne 1758)	Pa	Si-Pc	Ch	0.102	II

Af = African (Ethiopian)
Am = Asia minor
An = Angarian
As = Asian
Ba = Balcanic
C = Central
Ca = Caspian
Car = Carpathian
Ch = Chortobiont
Cos = Cosmpolitan
Da = Dacian
E = East
Eu = European
Fi= Fissurobiont
Da = Dacian
E = East
Eu = European
Fi= Fissurobiont

Geo = Geobiont
Il = Illyrian
Ir = Iranian
Ho = Holarctic
M = Mountain
Ma = Manchurian
Med = Mediterranean
Moe = Moesian
N = North
Pa = Palaearctic
Pan = Pannonian
Pc = Policentric
Po = Pontic
S = South
Si = Siberian
Th = Thamnobiont
Tu = Turanian
Tur = Turcesthanian

W = West

Relative abund.	Categories	
0.0625	I	rare
0.0626 - 0.1250	II	scattered
0.1251 - 0.2500	III	low frequent
0.2501 - 0.5000	IV	frequent
0.5001	V	common

Sampling were done by using standardized grassnetting method, which is common at comparative studies, and by thinning collection. To the quantitative analysis we applied cluster analysis on dominance-similarity, principal component analysis and non-metric multidimensional scaling, to describe the diversity we used diversity-ordering method (NUCOSA 1.05.06, Tóthmérész 1993). For the further proof of these results we have taken into account the given species association lifeform' and fauna-element type' distribution as well (Rácz 1998) (Table 2).

Results

From the 12 sampling sites 1610 individuals of 30 species have been collected (Table 3).

The main-component analysis (Fig.1) call our attention to the arrangability of samples, but the scattering of samples also suggest the possibility of arrangement from various standpoints.

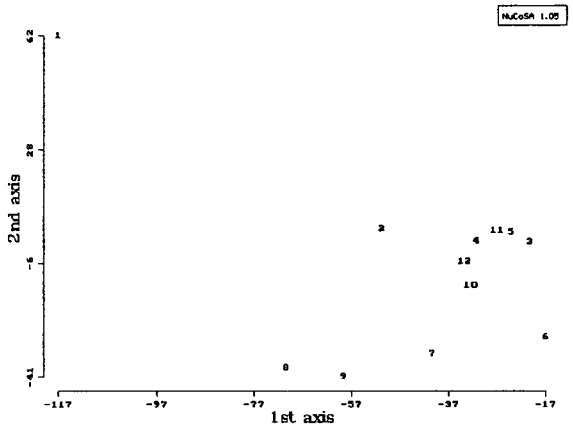

Fig. 1. Principal component analysis of sampling sites.

The results of the cluster analysis, which depends on the perturbance, are the followings (Fig.2):

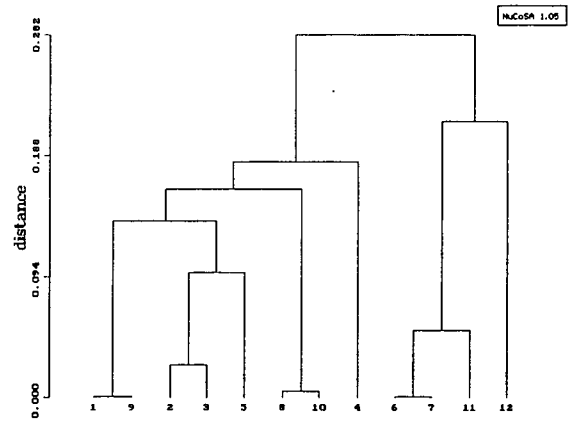

Fig. 2. Cluster analysis of sampling sites.

The first main group is highly heterogeneous. The common characteristic of the sampling sites belonging here is the strong perturbancy, which is caused by flooding in habitats on the inundation side (1, 2, 3, 4, 8), while on the protected side by the heavy grazing (9, 10) or extended crop cultivation and artificial fertilization (5). The second main group - sampling sites: 6, 7, 11, 12 - consists of only sites from the protected side, which were previously used for grazing, except No. 6. However, the regeneration of the sites have already been observed after quitting grazing.

The fact that the second main group consists of sites from the protected side, let us think that there should be a difference between the sites from the inundation are and the protected side. Using the non-metric scaling method, this difference can be shown (Fig.3), since the sampling sites from the inundation area (1, 2, 3, 4, and 8) forms a group, and the sites from the protected side (5, 6, 7, 9, 10, 11) forms an other distinct one.

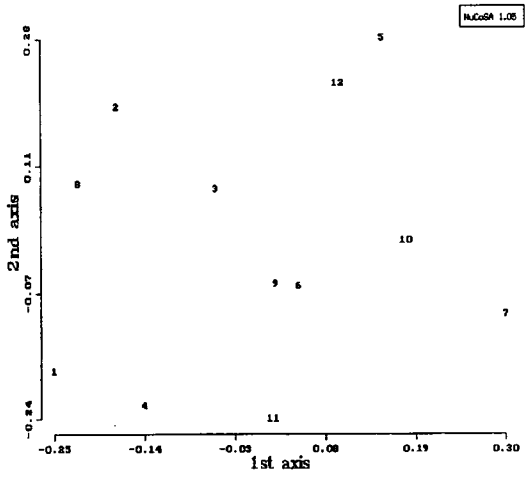

Fig. 3. Non-metric multidimensional scaling of sampling sites.

The diversity of the sampling sites from the inundation area (Fig.4) decreases from No. 8 towards No. 2, 4, and 3, while the site No. 1 cannot compare to any of them. The decreasing diversity well indicates the growing perturbancy. In case of the protected side we may conclude the same (Fig.5), since we found decreasing diversity to the direction of 9, 7, 12, 11, or 9, 6, 12, 11. The sample No. 10 and 5 can only be interpreted between themselves.

Discussion

From our results we can conclude, that there are no — in some ways — undisturbed grasslands can be found on the whole area. The sampling sites were influenced either by the flood, or were at a different stage of succession, or disturbed by human activities. In contrary to this, we found a relatively rich (25 % of the Hungarian orthoptera fauna) and diverse orthoptera community on the area (Table 2).

In the fresh, very humid grasslands the ratio of the predator Tettigonoida is high, in which the definitely thamnobiont-hygrophilous species are characteristic (*Conocephalus dorsalis, Ruspolia*

Table 3. Species of sampling sites

Species \ Sites	1	2	3	4	5a	5b	6	7	8	9	10	11
Phaneroptera falcata	0	2	0	0	0	4	6	7	3	0	0	0
Leptophyes albovittata	0	5	0	0	3	5	0	7	6	2	0	0
Conocephalus discolor	0	7	0	0	0	6	16	14	0	0	0	0
Conocephalus dorsalis	0	2	0	0	0	15	13	10	0	0	0	0
Ruspolia nitidula	0	2	0	0	0	2	1	3	0	0	0	0
Tettigonia viridissima	0	0	0	0	0	3	0	7	0	0	0	0
Decticus verrucivorus	0	0	0	0	0	2	0	6	0	0	0	0
Platycleis affinis	0	0	0	0	0	5	0	0	8	3	0	0
Bicolorana bicolor	5	0	0	0	0	0	6	4	0	0	0	0
Roeseliana roeselii	4	12	0	0	1	3	9	15	0	0	0	0
Gryllus campestris	6	3	0	6	6	0	4	5	8	3	5	5
Calliptamus italicus	0	0	0	0	0	0	0	0	31	25	0	0
Oedaleus decorus	0	0	0	0	0	0	0	0	4	0	0	0
Mecosthetus grossus	0	0	0	0	0	7	0	0	0	0	0	0
Parapleurus alliaceus	0	0	0	0	0	32	0	27	0	0	0	0
Chrysochraon dispar	8	7	0	0	0	7	1	16	0	0	0	0
Euthystria brachyptera	45	0	0	0	0	0	0	0	0	0	0	0
Stenobothrus crassipes	0	0	0	0	0	0	0	0	29	0	0	0
Omocestus ventralis	15	17	2	0	0	0	10	6	11	8	0	8
Omocestus haemorrhoidalis	0	0	0	0	0	0	0	0	4	0	0	0
Glyptobothrus biguttulus	13	0	14	14	16	0	7	9	12	11	0	12
Glyptobothrus brunneus	11	14	0	8	11	0	9	10	12	11	14	14
Glyptobothrus mollis	0	0	0	0	0	0	0	0	2	0	0	0
Chorthippus alobomarginatus	7	0	0	0	10	0	3	7	5	0	0	0
Chorthippus dorsatus	121	43	16	25	19	0	12	37	25	18	24	22
Chorthippus parallelus	13	19	11	16	7	25	48	61	55	22	11	22
Euchorthippus declivus	0	0	0	0	0	0	0	0	14	0	0	0
Dociostaurus brevicollis	0	0	0	0	0	0	0	0	16	9	0	0
Tetrix subulata	5	6	0	0	3	0	6	0	0	0	0	0
Tetratetrix bipunctata	0	5	0	0	0	0	2	6	5	0	0	0
	253	144	43	69	76	116	153	257	250	112	54	83

nitidula). Also the species of the characteristic chortobiont Acridoidea of these associations (*Chrysochraon dispar, Parapleurus alliaceus* and *Mecosthetus grossus*) are strongly hygrophilous. From this point of view, hardly any difference can be found among the sites from the inundated side and the less disturbed protected sites. With the decreasing humidity, and as the grassland structure becomes simpler, these species disappear, and those Acridoidea become dominant, which need at least seasonal hygrophilous environment at the early stage of their onthogenesis. On the other hand, the significant difference is very typical between the Orthoptera fauna of the less and the highly disturbed grasslands. The heavily grazed or intensively culti-

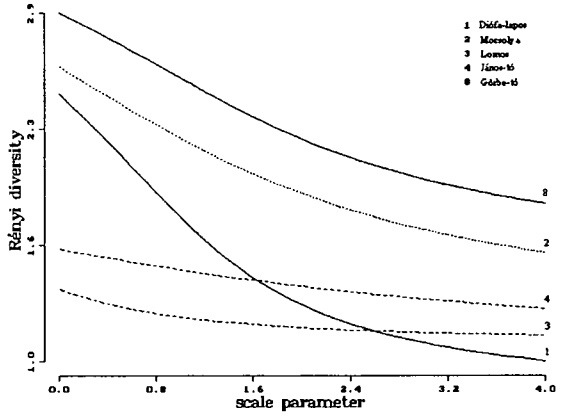

Fig. 4. Diversity ordering of sampling sites of the inundation area.

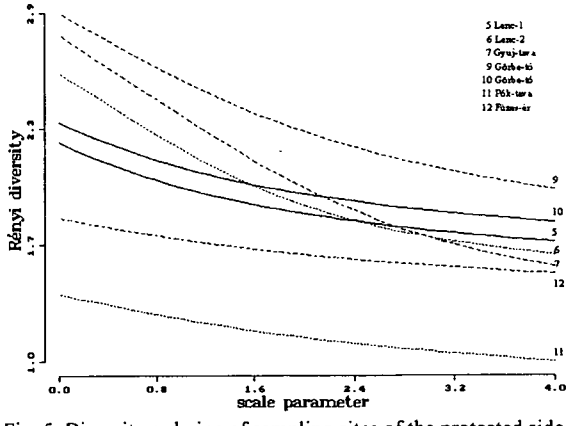

Fig. 5. Diversity ordering of sampling sites of the protected side.

vated grassland's Orthoptera species composition is quite poor, or can be characterized by one or two ubiquist species. This fact also call our attention to that the strong disturbance can extremely change the composition of the Orthoptera fauna (Rácz and Varga 1996).

Thus, this insect group is highly important not only from the point of view of fauna- and florahistory, but community- and productionbiology, that is indirectly economic and conservational point of view as well. Regarding the bioindicator value of this group, we can conclude, that using either the theory of physiological tolerance, or the theory of community answer as a starting point they are suitable for indication (Dorda 1998). Since, if we study the qualitative changes of the species composition, or the distribution of the high diversity frequency, we can point out the significant changes of features of the given area.

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TISCIA 31, 47-54

THE MALACOFAUNA OF THE TISZA VALLEY: INHABITATION AND SUBSEQUENT IMPOVERISHMENT

K. Bába

Bába, K. (1998): The malacofauna of the Tisza Valley: inhabitation and subsequent impoverishment. — *Tiscia 31, 47-54.*

Abstract. Recent flood areas restricted between dikes can be considered as the last refugia for the Tisza Valley biota, and also serve as ecological corridors for fauna dispersal. Sylvicultural management and poplar plantation, as the most severe human interventions, change the composition of river valley fauna, alter the direction of fauna migration, and homogenize the flood plain fauna. These finally lead to the irreversible degradation of the Tisza Plain biota. Poplar cultivation modifies microclimate, that also influences agricultural food production outside the dikes. Forestry practices produce numerous newly cut roads, along which the noxious weed *Ambrosia artemisiifolia* rapidly invades flood areas. Furthermore, poplar plantations are unfavourable for recreation activities and tourism. The processes of the Tisza's regulation and the drainage of the Great Hungarian Plain seems to be completed with accomplishing the once abolished plan for the canalization of the Tisza.

Key words: ecological corridor, fauna transport, species groups, species migration.

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Introduction

The issues exposed in the title will be approached through summarizing the results of a regional study on malacofauna. In this way, a comprehensive treatment will be given to the problems of fauna establishment and impoverishment.

Material and Methods

This summary is based on the author's more than 35 years of study on snail assemblages. During this, the absolute method was used with quadrats of 10×10×25 and 100×25×25 cm. All major forest and grassland community types in the Tisza Valley and on the Great Hungarian Plain were covered (Andó and Bába 1952, Bába 1969, 1973, 1975, 1976, 1977, 1980a,b,c,d, 1983a,b, 1989, 1991a, 1992a,c,d, 1993, 1994c, 1995). This overview was compiled as a result of the author's assignment to prepare UTM distribution maps for 97 snail species occurring on the Hungarian part of the Great Plain (Bába 1991a). For this, he used his own and literature data, and covered the most part of the malacofauna, as altogether 104 snail species inhabit the entire Great Plain (Bába and Kondorossy 1994). Several related works were also used for this analysis, like those by Radó (1967) and Pécsi (1969) to estimate the degree of forestedness and the hydrological status of the area recently and also prior to the regulation of riverways. The climatic districts by Kakas (1960), the physical geographical classification of Somogyi (1961), and statements of Andó and Vágás (1972) on river densities in certain areas (Bába 1982b) were also considered in the assessment of fauna distributions (Bába 1979a, 1982a,b). An area-analytical zoogeographical scheme of the Hungarian malacofauna was also prepared (Bába 1982a, 1989, 1992c), which enabled the evaluation of fauna distributions. Altogether 22 recent and Pleistocene faunas from fluvial sediments were analyzed (Bába 1979b). Further studies — lasting for two or more years — were conducted on the fluctuation and seasonal dynamics of snail assemblages in natural and managed forest stands (Bába 1980b, 1994a), and on the influence of poplar plantation in river flood plains on the snail fauna (Bába 1994b). The effects of forest management and hydrology on woodlands were studied by zoogeographical (Bába 1980, 1992b) and ecological methods through applying

species groups (Bába 1991b, 1992d, 1994a,b). Species groups used are as follows. Ecological groups: sciophilous (A) and photophilous (C) moisture demanding elements; swamp dwellers (B, the member Monacha species may also occur in muddy saline soils); species of open areas (D); riparian ubiquists (E). Habitat types: forest dweller (F); bush forest dweller (BE, indicates scrub formation); riparian species (RU); steppe dwellers (ST). Nutritional types: omnivore (O); herbivore (H); saprophagous (SZ).

The foregoing discussion can be divided into two main parts following the sequence of problems exposed in the title.

Inhabitation of the Tisza Valley

The malacofauna populated the Tisza Valley, and the Great Hungarian Plain as well, mostly by way of river transport. Several evidences support this theory. Thus, for example, the composition of the transported fauna changes in accordance with the species composition at river origins, as it was shown by studies on fluvial sediment snail assemblages (Bába 1979b). The Danube and Tisza rivers differ in the carried malacofauna. Rank orders of species in the fauna of Tisza deposits and in the snail assemblages establishing in willow thickets are similar. After grouping the Great Hungarian Plain collection sites according to physico-geographical subregions and then checking dissimilarities with χ^2 tests, clear differences appeared between the faunas of the Tisza Plain and the Dráva or Danube floodplains. This also confirms that the fauna of a given river valley is greatly influenced by the species composition at the river source.

Two groups can be distinguished among species occurring on the Great Hungarian Plain: a) ecological generalists of wide geographical distribution, and b) species restricted to former river beds or recent flood areas. From the latter group, forty eight species of subatlantic climatic character are listed in Table 1. These ecological specialists normally inhabit hilly areas in the Carpathian Basin, but occasionally occur on the Great Plain as well. Species were grouped according to the area-analytical zoogeographical classification, thus the directions of possible fauna transport events can be elucidated. These 48 species belong to 6 major and 17 subordinate fauna groups. They occur in inundation areas and former flood plains. The bottom chart displays the fauna groups carried by the Tisza and its tributaries, and the location of their probable entrance to the Great Hungarian Plain.

Table 1. Zoogeographical classification for 48 snail species of narrow ecological tolerance.

5.1. Illyrian
Aegopinella ressmanni (Westerlunnd 1883)
Aegopis verticillus (Ferrussac 1822)
Clausilia dubia (Draparnaud 1805)
Macrogastra ventricosa (Draparnaud 1801)
5.2.1. Trasian
Oxychilus glaber (Rossmässler 1835)
Oxychilus inopinatus (Illicny 1887)
Pomatias rivulare (Eichwald 1829)
5.2.2. Illyro-Moesian
Balea biplicata (Montagu 1803)
Clausilia pumila (C. Pfeiffer 1828)
Daudebardia rufa (Draparnaud 1805)
Laciniaria plicata (Draparnaud 1801)
Malacolimax lenellus (O. F. Müller)
Perforatella incarnata (O. F. Müller 1774)
Tandonia budapestiensis (Hazay 1881)
Trichia hispida (L. 1758)
Vitrea diaphana (Studer 1820)
6. Adriato-Mediterranean
Chilostoma planospirum (Lamarck 1822)
Cochlodina laminata (Montagu 1803)
Discus rotundatus (O. F. Müller 1774)
Lehmania marginata (O. F. Müller 1774)
Limax cinereoniger (Wolf 1803)
Vitrea crystallina (O. F. Müller 1774)
7. Atlanto-Mediterranean
Arion ater (L. 1758)
Arion fasciatus (Nillson 1823)
Arion sylvaticus (Lohmander 1937)
Cepaea hortensis (O. F. Müller 1774)
Cepaea nemoralis (L. 1758)
8. Holo-Mediterranean
Cecilioides aciculata (O. F. Müller 1774)
Ena obscura (O. F. Müller 1774)
Lehmania nyctelia (Burguignat 1861)
Limax flavus (L. 1758)
Limax maximus (L. 1758)
Oxychilus draparnaudi (Beck 1837)
Oxychilus hydatinus (Rossmässler 1838)
Vertigo moulinsiana (Dupuy 1849)
Vertigo pusilla (O. F. Müller 1774)
Vitrea contracta (Westerlund 1871)
9.1. Carpathian
Perforatella dibothrion (M. V. Kimakowicz 1884)
9.2. Carpatho-Sudetian
Bielzia coerulans (M. Bielz 1851)
Perforatella vicina (Rossmässler 1842)
9.3. Carpatho-Baltian
Perforatella bidentata (Gmelin 1788)
9.4. Alpo-Carpathian
Isognomostoma isognomostoma (Schröter 1784)
Perforatella umbrosa (C. Pfeiffer 1828)
Trichia unidentata (Draparnaud 1805)
9.5. Daco-Podolian
Chilostoma banaticum (Rossmässler 1838)
Hygromia transsylvanica (Westerlund 1876)
Hygromia kovácsi (Varga et Pintér 1972)
10.1 Boreo-Alpine
Arianta arbustorum (L. 1758)

Thus, it can be stated that the number of species transported by running waters is positively correlated with the river density of the area and the water discharge of rivers. Similarly, there are differences

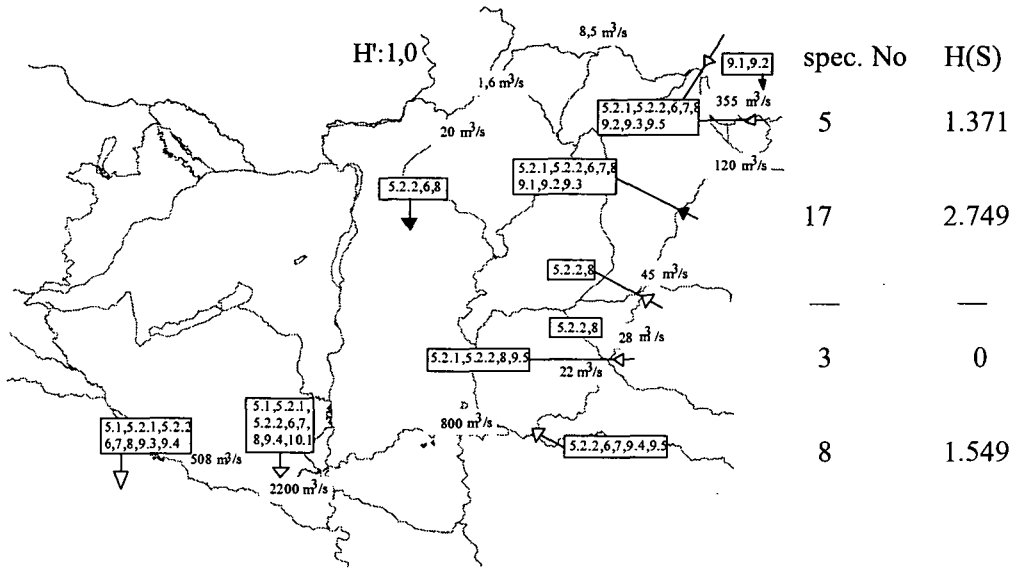

Fig. 1. Geographical distribution and localities of entrance to the Great Hungarian Plain for 48 stenoecic snail species. River discharge figures and diversity of water-carried snail assemblages are also shown.

between rivers in the diversity of water-carried species. Snails typical of hilly regions may invade certain forested parts of the Great Plain as well, e.g. the Gödöllő Hills, or the Bátorliget and Déda Forest sites on the Szatmár-Bereg Plain (Fig. 1). This zoogeographical phenomenon is termed between-forest dispersal, in which 24 % of the species is involved.

Historical factors may also influence the current distribution of organisms. The continuous occurrence of *Punctum pygmeum* since the Würm glaciation has been demonstrated by Krolopp and Sümegi (1991). Island-like gallery and swamp forests appearing along former Danube beds and wave areas preserved five species (e.g. *Vertigo pusilla* and *Perforatella incarnata*) typical of the Danube Valley. In the Tisza Valley, *Perforatella vicina* is such a relic species.

The flood plain of the Tisza and its tributaries might have extended from Kiskunfélegyháza to Debrecen, as reconstruction revealed. Following river retreat, large water surfaces remained behind, greatly enhancing the dispersal of riparian ubiquist species of wide geographical distribution. Most of these snails are common even today. Such ubiquists are e.g. the amber snails (*Succinea* spp.), and *Zonitoides* and *Bradybaena* species. Large areas of the Plain were covered by water permanently or temporarily several decades ago. These open water surfaces mostly disappeared by now as a consequence of drainage or melioration. With this, the list of causes behind fauna impoverishment have already started.

Causes of malacofauna impoverishment in the Tisza Valley

Drainage and regulation of riverways started in the 1840s in the Tisza Valley. As a consequence, the ground water table level — formerly being close to the surface — has dropped to 4-6 m deep at some places by the sixties. Recently, this unfavourable process has expanded to most parts of the Great Plain, thus changing the conditions for fauna dispersal markedly.

A peculiar feature of the Tisza Valley is the absence of an autochtonous malacofauna. Consequently, the region is inhabited by fauna elements arriving from other areas and establishing permanently or temporarily. Mostly forests providing sufficient moisture and food source are appropriate for the establishment of newcomers. This process might have operated until the previous century, as it can be inferred from the reconstructed vegetation map given by Zólyomi. Even in the 1920s, five species of montane character (including a *Clausilida* sp.) were recorded at Dorozsma Bath by Czógler (1914-36).

On the flood plain, the distribution of species with montane affinities among forest types was as follows: 67% in gallery forests, 47% in willow-poplar woods and 33% in hornbeam-oak woods. Most of these forests have been cut down by now. According to a recent survey by the WWF, gallery forests make up some 3% of the flood plain woods (Dobrosi et al. 1993). Most of these have survived at

the Upper and Middle Tisza Reaches. Changes in the degree of forestedness and amount of precipitation in the catchment area of the Tisza water system determine the conditions of fauna colonization. River discharge is also influenced. The role of the four to five annual floods in fauna transport and selection might have been substantial before the source areas have been deforested. This intervention itself decreased considerably the abundance and diversity of the alluvial fauna.

Deforestation in inundation and reclaimed areas prevents the dispersal of river-carried fauna. This influence is especially serious if we consider that the continental climate of the Great Hungarian Plain hampers the spread of snails in the absence of forests and wet soil. Climatic districts A1-A5 (Kakas 1960) of the the Great Hungarian Plain are characterized by an arid, hot or moderately hot summer.

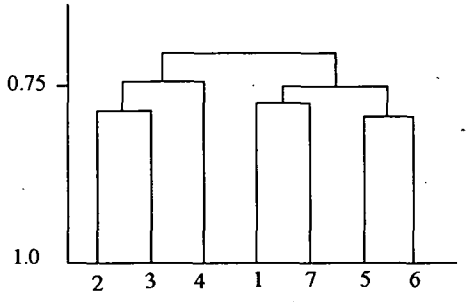

Fig. 2. Classification of Tisza Plain regions on the basis of fauna elements (study sites are listed in Table 2).

Snail dispersal is further limited in reclaimed areas by various human activities, like canalization, regular cutting of dikes for hay making, drilling drinking water wells, construction of the two barrage systems on the Tisza, establishment of recreation facilities, and agricultural production in flood areas. All these alter microclimatic conditions.

As the water chemistry deteriorates in the Tisza and its tributaries, the number of species with living river-carried individuals decreases gradually. This is the reason of the zero snail species diversity transported in the polluted Sebes Körös river.

Current distribution of the Tisza Plain malacofauna

The recent allocation of the Tisza Plain snail fauna is shown in Table 2. and Fig. 2. as the result of a cluster analysis on zoogeographical categories arranged according to geographical subregions. In this, the Nyírség (2), and the Upper and Middle Tisza Regions (3 and 4) form one cluster core. These areas are relatively rich in forests, especially in gallery forests. The other cluster core is made up by two pairs of regions: one is the level alluvial fan of the Northern Great Plain (1) and the Körös-Maros interfluve (7), while the other is the Lower Tisza Valley (5) and the Körös Region (6).

Table 2. Distribution of zoogeographical fauna groups among the Tisza Plain regions. The associated cluster diagram is also shown below.

Fauna groups	1	2	3	4	5	6	7
East Siberian	3	9	8	9	6	5	4
West Siberian	1	3	2	2	2	1	1
Euro-Siberian	0	2	2	3	1	1	2
Holarctic	4	8	8	7	7	5	5
Turkestanian	1	1	1	1	1	0	1
Kaspo-Sarmathian	2	3	2	2	2	2	2
Ponto-Pannonic	2	3	2	2	1	1	1
Daco-Podolian	1	1	2	1	0	1	2
Trasian	3	5	2	1	1	1	2
Illyro-Moesian	3	3	4	3	0	0	2
Adriato-Mediterranean	1	4	5	0	2	0	2
Atlanto-Mediterranean	1	2	2	0	0	2	0
Holo-Mediterranean	6	14	7	6	5	6	3
Carpathian	0	0	1	0	0	0	0
Carpatho-Sudethian	0	1	2	1	0	0	0
Carpatho-Baltian	0	2	1	0	0	0	0
Alpo-Carpathian	0	0	1	0	0	0	0
All species (fauna elements)	28	61	52	38	28	25	27

Study sites were: 1. Alluvial fan of the Northern Great Plain; 2. Nyírség (Samicum); 3. Upper Tisza Region; 4. Middle Tisza Region; 5. Lower Tisza Region; 6. Körös Region; 7. Körös-Maros Interfluve

This pattern mainly reflects local watercourse frequencies and climatic properties in the catchment area of the tributaries. In addition, regions in the second cluster core are homogenized by anthropogenic effects. In these areas (e.g. the Northern Great Plain, and the foothills of the Mátra and Bükk Mts.), forest cover is very low, the proportion of arable land is quite high and the climate is relatively arid. Low species number characterizes these latter four regions. Human impacts tend to homogenize the differences between them, although they can still be distinguished by several differential species surviving in refugia. Most species are holarctic ubiquists, although the proportion of Turkestanian Ponto-Pannonic and Daco-Podoloian steppe dweller elements is also high. European montane (Carpathian and Carpatho-Sudetian) and Atlanto-Mediterranean components are completely missing, just like the Illyro-Moesian species in the Lower Tisza and Körös Regions. A reciprocal behaviour of continental and subatlantic fauna groups characterizes areas 2, 3 and 4, composing the first cluster core. Also here, a lower ratio of montane Ponto-Mediterranean fauna group, and a higher preponderance of Siberian-Asian elements and steppe dwellers are typical. In the Lower Tisza Region, the proportion of Holo-Mediterranean steppe dweller components increases.

The environs of Tiszadob on the border of the Upper and Middle Tisza Regions deserve special attention, as four rivers (Takta, Sajó, Hernád and Tisza) join there. Extensive gallery forests occur along the Tisza, but not on the streamside of the three affluents. These forests are under forestry management in inundation areas. As a consequence, Central European montane elements (represented by the Carpatho-Baltic *Perforatella bidentata*) have become sporadic in their species composition. Alien synantropic slugs (*Arion hortensis, Limax maximus*) appear in gallery forests as a result of human influence.

The most serious threats for the survival of snail populations that have already established in inundation areas are clearcutting of forests, sylvicultural management and poplar plantation extensified in the past few years.

Impacts of forest management and poplar plantation

Bagiszeg in the Upper Tisza Region and Landor in the vicinity of Makó (both are protected areas) have identical malacofauna (Bába 1995). The former site has an oceanic-like climate with mild summers, while the latter is of a continental character with dry summers. Willow woods were cut down around Bagiszeg in 1969, where agricultural fields proceeded down to the forest margin. A major flood reached this area in 1970, that was followed by a *Lymantria* damage in 1973 and a stand thinning by forestry to increase timber production in 1984. At Landor, a moderate thinning took place in 1989. The influence of these events on snail assemblages was studied by following the fate of three species groups (Bába 1994). Results are shown in Fig. 3.

Despite major environmental changes, the relations of the reciprocal photophilous and sciophilous groups had not changed at Bagiszeg, where the climate is mild. The dominance of forest dwellers (F) within habitat types, and that of omnivores (O) among nutritional classes has been regenerated.

Sylvicultural management caused serious structural changes in snail assemblages at Landor, where the climate is more arid. Terrestrial eutrophication occurred as the following groups became dominant: riparian ubiquists typical of willow-poplar woods

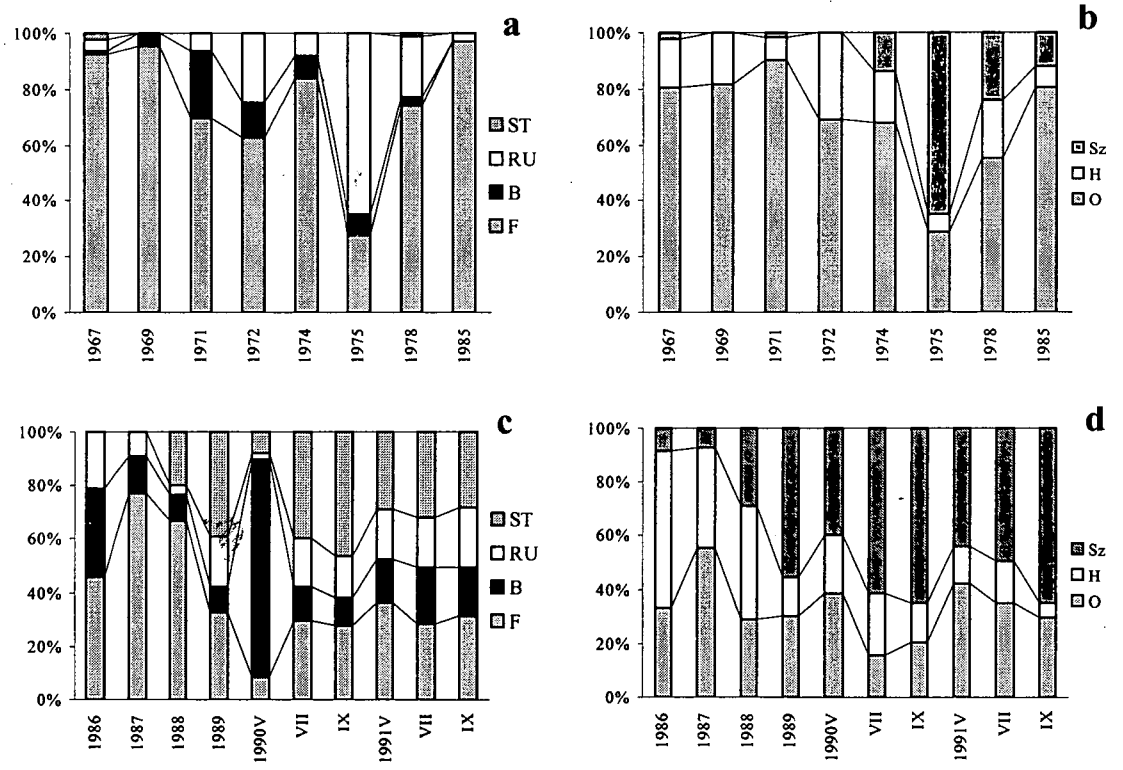

Fig. 3. Distribution of snail species among habitat types (a,c) and nutrition types (b,d) in Bagiszeg (a,b) and Landor (c,d). Habitat types. ST: steppe dweller; RU: riparian ubiquist; B: bush forest dweller; HP: hygrophilous swamp dweller. Nutritional types: SZ; saprophagous; H: herbivore; O: omnivore.

among ecological species groups, steppe dwellers (ST) among habitat types, and saprophagous species (SZ) among nutritional types.

The slow impoverishment of the fauna over the last 100 years has been crowned by the impacts of poplar plantation in wave areas that accelerated in the past few years.

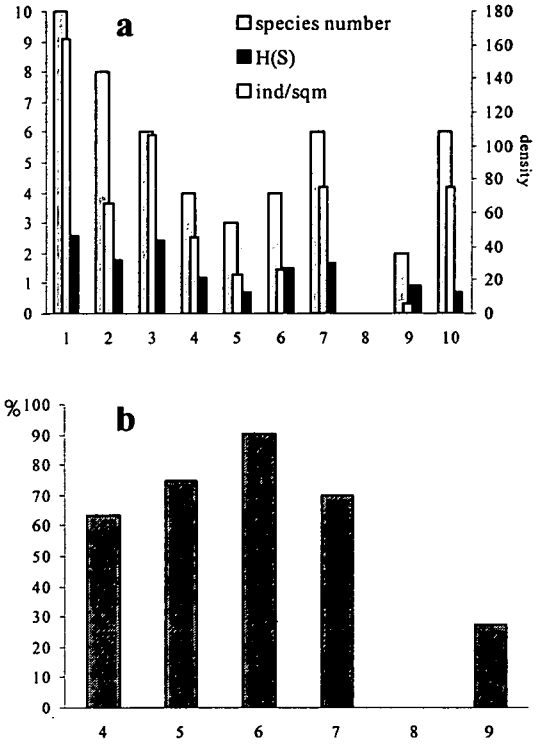

Fig. 4. Regional studies in the Middle Tisza Landscape Protection District; species number, diversity and abundance values are presented in par **a**; lower figure (**b**) shows the proportion of living individuals compared to all specimens. Number of stands: Upper Tisza 1: estuary of Szamos, 700 rkm of Tisza; 2: Tiszalök, 690 rkm; Middle Tisza 3: Kisköre, Borzanat, 403 rkm; Middle Tisza Landscape Protection District 4: *Saliceetum albae-fragilis* — Besenyszög; 5: *Saliceetum albae-fragilis* — Tiszasüly; 6: willow-locust-ash forest, Tiszasül;y; 7: *Saliceetum albae-fragilis* — Péj; 8: oak plantation, Besenyszög; 9: old poplar plantation, oxbow lake at Kanyas; 10: Lower Tisza, Mártély.

The influence of new poplar forests was investigated within the Middle Tisza Landscape Protection District, along river reaches upstream of Szolnok, and at Algyő. In this protected landscape, the original willow-poplar woods have been turned into cultivated poplar plantations. The consequences of this intervention are reflected at the regional level in the decline of abundance, diversity and individual density, and in the higher proportion of dead specimens (Fig. 4). Collection sites 1-3 in the Upper Tisza Region, and site 10 in the Lower Tisza Valley are control plots studied in previous years.

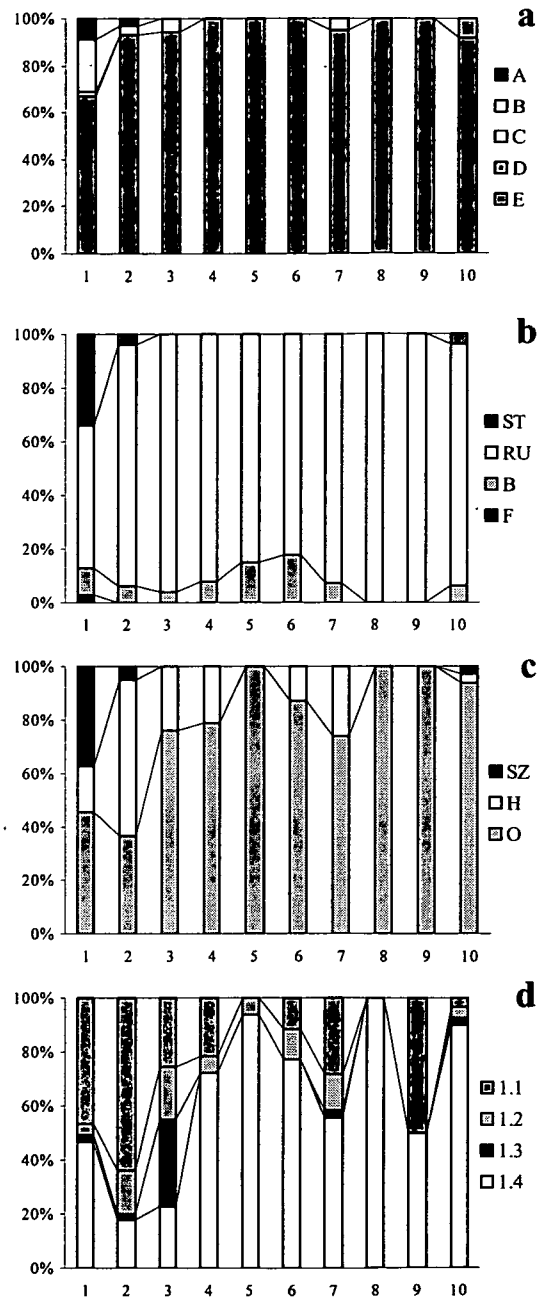

Fig. 5. Proportion of ecological groups (**a**), habitat types (**b**), nutritional types (**c**) and fauna elements (**d**). (For numbers of samplig sites see Fig. 4, and for legends of **b** and **c** see Fig.3). Ecological groups: A: sciophilous; B: swamp dweller; C: photophilous; D: species of open areas; E: riparian. Zoogeographical classification: 1.1. East Siberian, 1.2. West Siberian, 1.3. Euro-Siberian, 1.4.

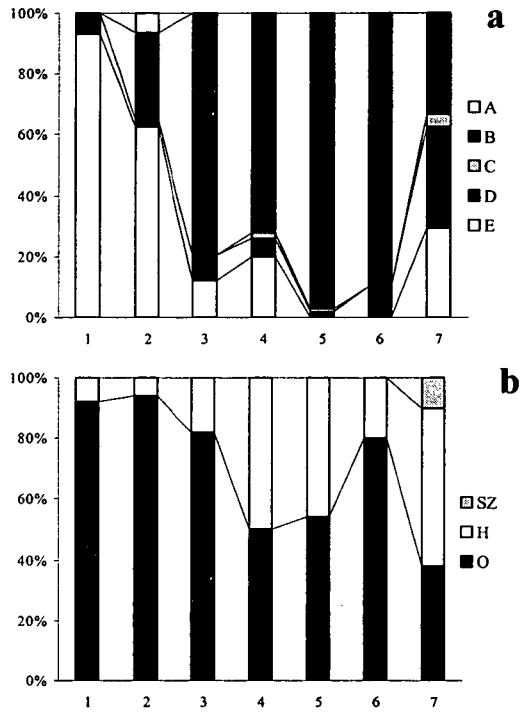

Fig. 6. Distributions of ecological species groups (**a**) and nutritional types (**b**) at Algyő in the area between riverbed and dike (for legends see Figs 3 and 5; codes of samplig sites are listed in Table 3).

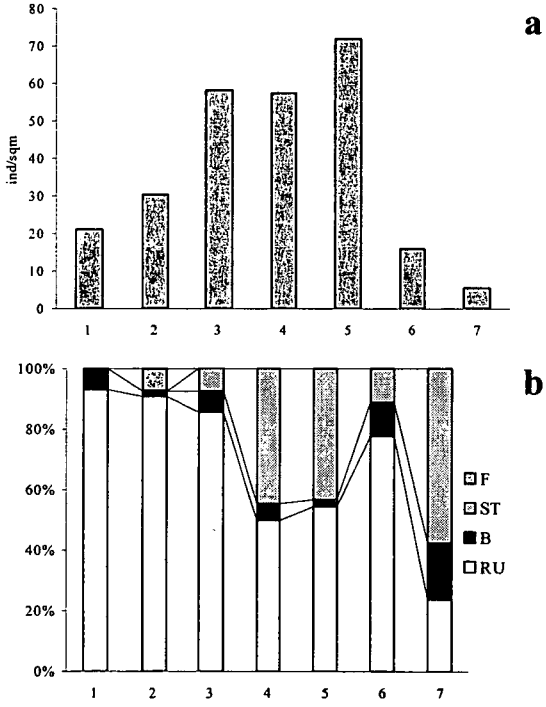

Fig. 7. Distributions of abundance (a) and habitat types (b) at Algyő in the area between riverbed and dike (for legends see Fig. 5; codes of samplig sites are listed in Table 3).

Changes in species group distributions were associated with the decrease of snail diversity (Fig. 5). Riparian ubiquist (E and RU) and omnivorous (O) snails became abundant, while in the zoogeographical composition holarctic ubiquist species (1.4) prevail.

A four-year study running from dike-foots to river margin at Algyő elucidated the role of middle-inundation area poplar plantations in the changes of the malacofauna (Table 3, Figs 6 and 7). In these figures, collection site 1 is located within a willow-polar forest at the dike, while plots 6 and 7 are from a willow thicket bordering the Tisza. Sites between these are situated within young or old poplar plantations, or in thickets common around digout pits or poplar cultivation. According to these, swamp dwellers (B) predominate among ecological species groups (Fig. 6), represented by the Holo-Mediterranean *Monacha carthusiana*. Concerning nutritional types, herbivores (H) gain a dominant role, as cultivated poplar stands and bordering thickets have a rich undergrowth.

Table 3. Proportion of species migrating from the direction of the Tisza and of the dikes at Algyő.

	1	2	3	4	5	6	7
Species migrating from the direction of the Tisza							
Perforatella rubiginosa		1				1	
Cochlicopa lubrica	1					1	
Succinella oblinga	1	7					
Succinea putris	1	1	15	9	1	28	2
Zonitoides nitidus		15	3				4
Σ	3	24	18	9	1	29	6
%	75	89	39	31	4	80	86
Species migrating from the direction of the dike							
Limax maximus	1	1					1
Monacha carthausiana		1	24	15	9	5	
Cepaea vindobonensis			4	3	18	1	
Vallonia costata		1					
Helix pomatia				2	1	1	
Σ	1	3	28	20	28	7	1
%	25	11	61	69	96	20	14

1. *Salicetum albae-fragilis*; 2. aged poplar forest; 3. young poplar forest; 4. digout pit; 5. *Amorpha* scrub; 6. willow-poplar wood with *Urtica*; 7. *Salicetum triandrae*.

The distribution of abundance (ind/m^2) values shows that few species occur with relatively high abundance in flood areas under human influence (Fig. 7). Among habitat types, steppe dweller species (ST) dominate in the altered vegetation. Their dispersal into inundation areas is enhanced by thickets along forest openings and alleys. Species migrating from direction of the Tisza and of the dike behave in a reciprocal way, as it appears in Table 3. Steppe dweller species can even reach the river.

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TISCIA 31, 55-58

SPAWNING OF THE EUROPEAN MUDMINNOW (*UMBRA KRAMERI* WALBAUM) IN THE BASIN OF THE RIVER ÉR

A. Wilhelm

Wilhelm, A. (1998): Spawning of the European mudminnow (*Umbra krameri* Walbaum) in the basin of the river Ér. — *Tiscia 31, 55-58.*

Abstract. The European mudminnow reaches its maturity at the age of two years. It spawns in May and June in the Ér basin.
The number of the forming eggs in the 3rd maturing stage ranges from 626 to 2689 depending on the age of the fish. Literature data show much less eggs than above. The reason of the difference is that a great number of eggs are absorbed in the 4th maturing stage.
A similar phenomenon can be observed at the brown bullhead (*Ictalurus nebulosus*) which guard the eggs and the descendants, too. It is probable that this is the physiological background of the switch from the wide-spread r-selectionist reproduction strategy to K-selectionist strategy, characteristic of the egg-guarding fishes.

Key words: maturing stage, egg number, egg guarding, r-K selectionist strategy.

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Introduction

The river Ér (Ier) flows in a ditch with a direction NW-SE in the NW region of Romania between the rivers Kraszna (Crasna) and Berettyó (Barcău). It flows into the river Berettyó on the territory of Hungary.

In the lightly inclining basin there formed a slowly flowing marsh with little islands and backwaters which offered the mudminnow ideal circumstances for life. After the draining of the region finished in 1972, the conditions of existence of the species grew narrow, but in spite of these facts the patches of the remained marshes and the connecting canals made possible the surviving of the fish.

There are different data concerning the eggs in the works of, in the one hand, Geyer (1940), Pintér (1975) and Bota (1981), and on the other hand Makarov (1936) and Pavlov (1953). Our previous observations were closer to the latter ones (Wilhelm 1987).

Material and methods

Samples were gathered between 1973 and 1995 with a scratching net. This is the single successful fishing instrument to lift out this fish with mud because it is very cautious, and hides in the mud at the smallest disturbance.

The sampling sites are indicated on Fig. 1. At the 3rd site fish was sampled in each months.

We measured the total and standard (without the caudal fin) length and the weight of the individuals. The age of the fishes was determined from the annual rings of the scales. The scales were cleaned in thin hypochlorite solution, and then studied with stereomicroscope. We took out the ovaria of the fishes, measured their weights, than counted those eggs that were at least in the 3rd maturing stage and were visible to the naked eye. Since there were not very many eggs, we did not apply the method of recounting after the tests, we counted directly the eggs.

The maturing stages of the eggs were determined with the Nikolski's (1963) method.

Results and discussion

We found that both the males and females reach their sexual maturity at the age of 2 years. At this age their standard length is approximately 50 mm, their weight is 2 g (Table 1). This corresponds to the literature data (Pintér 1975, Botta 1981), although in Pavlov's opinion (1953) on the Lower Danube the mudminnow reaches these dimensions at the age of one year, and in his opinion this species becomes mature at this age. So the reaching of maturity does not depend on age but on dimensions.

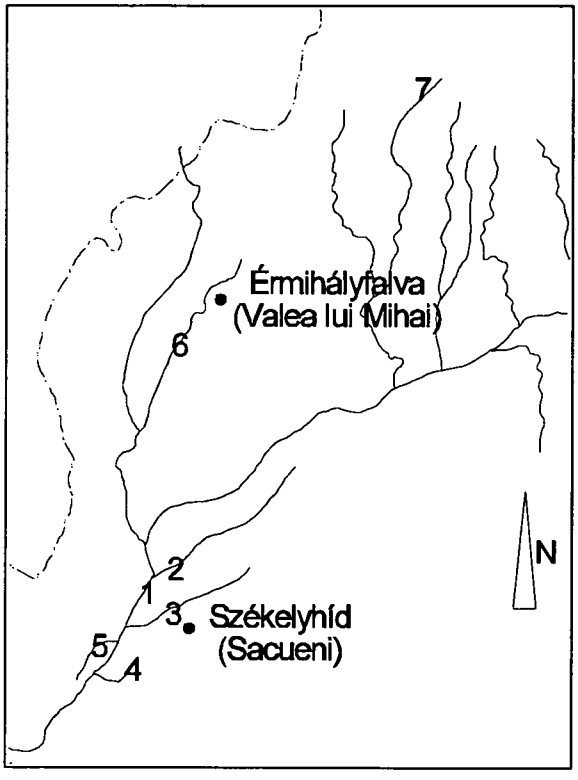

Fig. 1. Location of sampling sites. 1. Ér bed near Székelyhíd (Săcueni); 2. Draining branch near Kiskereki (Cherechiu); 3. The former main course of Ér near Székelyhíd; 4. The former backwater of Ér near ágya (Cadea); 5. The old backwater near Csokaly (Ciocaia); 6. Brook Móka (Mouca) near Érsemjén (Simian); 7. Boggy marsh near Reszege (Resighea).

Table 1 shows the distribution of standard body length and weight according to sex and age, and it indicates the length and weight of different age-groups. It can be seen that the dimensions of females exceed those of males.

Concerning the division of sexes, it is noticeable that at a younger age there are more males than females, but this proportion changes soon. The age reached by females exceeds the age of males. A five years old male is very rare, but we found even seven years old females.

Studies concerning the maturing of the eggs show that the growth of ovocytes starts immediately after the spawning, but at younger generations these remain in the 2nd maturing stage during winter. The older, 5-6 years old individuals reach the 3rd maturing stage in November-December, so their eggs are visible to the naked eye and they can be counted easily. This stage is reached by the younger generations only in February. The reaching of the 4th maturing stage is at the end of April and early May at every generations.

As it was mentioned earlier, there are very different data concerning the number of eggs. Pavlov (1953) had found a number of 835-1666 eggs at the population living on the Lower Danube, while in Makarov's opinion (1936, quoted by Pavlov), the number of the eggs varies between 1582 and 2707. On the other hand, Pintér (1975) mentioned 100-200 eggs. According to Geyer's observations (1940) an 8 cm long female spawned 214 eggs in laboratory conditions. Botta (1981) reports 75-80 spawned eggs in aquarium.

Our observations concerning the number of the eggs in the 3rd maturing stage are summarized in Table 2. Consequently the number of the eggs found in a female varies between 626 and 2689, and it shows considerable individual differences. We found the increase of the egg number with age, the common phenomenon of fish.

Therefore there is a considerable difference between the number of eggs found in the dissected fishes and the number of the spawned ones. The interpretation is given by studying the ovaria of the fishes reached the 4th maturing stage. In this period a great just before spawning there were counted 149 mature eggs with diameters of about 2 mm and 313 eggs which were visible to naked eye, but they could be counted only under the microscope.

In this stage the ovaries are somewhat similar to the ovaries of those fishes which spawn several times every year, but the mudminnow spawns once a year, and after spawning their ovaries are full of ovocytes showing typically the 2nd maturing stage.

We found a similar phenomenon of spawning of the brown bullhead (Wilhelm 1979, 1980).

According to our observations in the Ér basin, the mudminnow spawns in May and June. The temperature of the water necessary to the spawning was 12.5-16 °C by Geyer (1940), 12-18 °C by Balon (1967) and 20 °C by Botta (1981), but they mention a spawning in April. In April we measured 8-11 °C water temperature in the Ér basin, and even the average air temperature varied between 9.2-12.8 °C

Table 1. Distribution of standard bodz length and weight according to sex and age.

Age	Sex	Standard length (mm)		Weight (g)		n
		Average	Extreme values	Average	Extreme values	
2-2+	male	49.8	43.5-56.0	1.71	1.42-3.85	47
	female	49.7	44.0-57.0	2.38	1.14-3.10	41
3-3+	male	56.1	51.0-69.5	3.24	2.67-3.95	9
	female	57.4	53.0-68.5	3.40	2.73-5.06	20
4-4+	male	67.4	62.0-74.5	6.11	4.17-8.24	5
	female	67.7	60.0-78.5	5.37	3.90-7.95	8
5-5+	male	72.0	—	6.78	—	1
	female	77.0	72.0-88.5	8.69	7.22-11.25	9
6-6+	male	—	—	—	—	—
	female	85.3	80.5-89.0	14.22	11.18-18.21	5
7-7+	male	—	—	—	—	—
	female	101.0	100.0-102.0	23.72	19.67-27.78	2

in the study years, and it got warm to 12.7-18 °C only in May. Considering these data, it can be ascertained that our observations correspond to the literature data, because the time of spawning is mainly determined by the water temperature.

Table 2. Distribution of the egg numebr in the 3rd maturing stage• according to age.

Age	Number of eggs		n
	Average	Extreme values	
2	854	699-1271	4
3	843	626-1415	10
4	1780	1027-1877	4
5	1548	1059-2290	9
6	2190	1514-2689	5
7	2465	—	1

It would be very difficult to observe the elements of behavoiur concerning the spawning of the mudminnow in the water of marshes and swamps. But it was visible that the specimens caught in the spawning time, both males and females, were brightly coloured. Their colour was golden and gleaming decorated with longitudinal whitish streaks on their abdominal part. The colour of the older specimens was quite dark brown, and on the dark background the light streaks were more effective.

In August at the 8th sampling site we caught descendants at the sunny parts of the clumps in the marshes, on the parts which stood near the open water surface. It is probable that the nests were there, as well, and they were not in the shady water which gets warm slowly among the clumps. We always caught mature females with the descendants, this points to a descendant-guarding behaviour although this was not mentioned earlyer from the laboratory studies.

Concerning the seasonal migration of the species, the monthly repeated fishings at the 3rd sampling site show (Table 3) that mainly young, immature individuals migrate. During autumn the young animals disperse and only the mature part of the population remain in the place sharing the hiding places. Therefore in spring the spawning pairs nead not devote much energy to the division and protection of the territory.

Table 3. Dynamics of the mudminnow according to sex and age at the 3rd sampling site.

Time of sampling	juv.	male	female	Sum
16 September 1983	26	7	2	35
4 October 1983	35	4	11	50
2 November 1983	12	9	11	32
12 November 1983	8	—	1	9
18 November 1983	—	2	3	5
20 December 1983	—	3	8	11
29 December 1983	3	1	7	11
13 January 1984	—	2	2	4
3 February 1984	4	6	8	18
21 February 1984	—	3	1	4
25 February 1984	—	8	6	14
10 March 1984	—	1	2	3
10 April 1984	—	2	2	4
4 May 1984	—	—	2	2
16 May 1984	2	2	—	4
11 June 1984	—	2	1	3
18 June 1984	—	—	1	1
6 July 1984	—	5	5	10

Conclusion

In the Ér basin the mudminnow spawns in May and June. Probably the time of spawning depends mostly on the water temperature. The spawning happens in pairs, so it is not necessary to the whole population to be synchronized. This must be the reason of the relatively long spawning period, but every individual spawns only once a year. The spectacular difference between the number of forming and spawned eggs can be explained by the regress and absorption of a great part of the eggs in the 4th maturing stage. During the maturation a certain number of the eggs are absorbed at each species, but at the mudminnow this process is very considerable. A similar phenomenon can be observed at the brown bullhead, which guards the

eggs and descendants, too. We think that this is the physiological background mechanism of the change from r-selectionist reproduction strategy to K-selectionist strategy. While the former one is characteristic of the greatest number of the fish species, the latter can be found only at the guarders of eggs and descendants.

Acknowledgement

The air temperature data originated from the Agrometeorological Office of Săcueni. I appreciate their help very much.

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TISCIA 31, 59-61

SEASONAL DYNAMICS OF CARP INFESTATION BY *TRICHODINA NOBILIS* CHEN. 1963 (PERITRICHA, CILIATA) IN TWO FISH-PONDS IN BANAT

V. P. Nikolić and P. D. Simonović

Nikolić, V. P. and Simonović, P. D. (1998): Seasonal dynamics of carp infestation by *Trichodina nobilis* Chen. 1963 (Peritricha, Ciliata) in two fish-ponds in Banat. — *Tiscia 31, 59-61.*

Abstract. Comparison of the fish-pond carp infestation by *Trichodina nobilis* revealed significant seasonal differences in two fish-ponds from Banat. These differences originated from the bimodal seasonal dynamics of *Trichodina*, since the highest values of infestation were observed in Spring and Autumn.

Key words: parasite, bimodal dynamics.

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Introduction

The study of parasitic ciliates of the freshwater fish, and especially those of the fish-pond carp, has not yet been carried out in details in Yugoslavia. Results of similar investigations have been reported from Bulgaria (Golemansky and Grupcheva 1975, Grupcheva and Golemansky 1986), Czech Republik and Slovakia (Ergens and Lom 1970, Lom 1970, Lom and Dykova 1984, 1989), states of the former USSR (Stein 1982, Allamuratov 1986, Majorov and Goncharov 1987, Naumova 1987), Great Britain (McCallum 1982), Germany (Werner 1982, Walter 1988), South Africa (Basson and Van As 1989) and Canada (Poulin 1991). These investigations are of great theoretical and practical importance as Ciliate parasites are the commonest parasites of the fish reared in our country.

Material and methods

Material was collected from the Ečka and Uzdin fish-ponds during the March-October period in 1993. The Ečka fish-pond is situated at the alluvial plain between River Tisza and River Begej, while the Uzdin fish-pond lies along River Tamiš. A total of 346 carps of first year was used for the analysis, 166 of which were mirror carps and 180 scaled cars. From the living samples squash slides were taken and observed under light microscope (600×) after standard silver impregnation. Difference of infestation was examined by Kruskal-Wallis H test (Sokal and Rohlf 1981).

Results and discussion

The species *Trichodina nobilis* can be observed in the Ečka fish-pond during nearly the whole year (Fig. 1). The largest infestation was observed in Spring (March 36.67%, April 46.15%), and its degree decreased during the year. In May, August

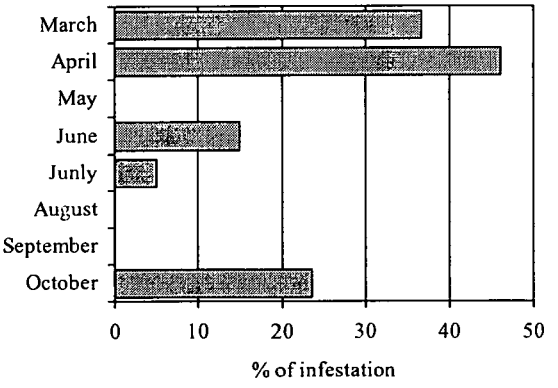

Fig. 1. Seasonal dynamics of infestation rate in the Ečka fish-pond.

and September the parasite was absent, but it appeared again in October (23.81%) when the water temperature was lower.

In the Uzdin fish-pond *Trichodina nobilis* occurred in March at a rate of 14.81%, in April the degree of infestation increased to 25.00%. Similarly to Ečka fish-pond, this parasite was not observed in May. It was present again in July (24.14%). The percentage of infestation fell to 4.17% in August. The species was absent in September, while it performed an abundant appearance (36.36%) in October. Later value was the greatest in this fish-pond (Fig. 2).

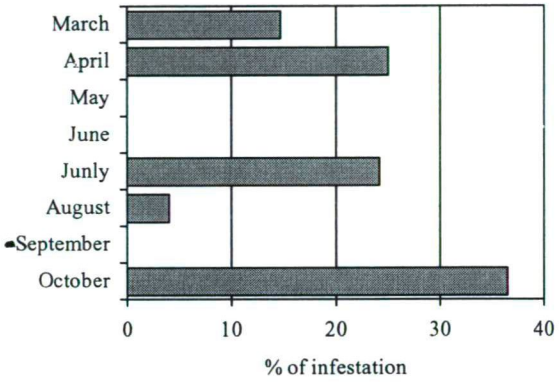

Fig. 2. Seasonal dynamics of infestation rate in the Uzdin fish-pond.

Trichodina nobilis (Fig. 3) occurred in 20% of carp specimens of our fish-ponds during the whole year. It was introduced with grasscarp (*Ctenopharyngodon idella*) from China and the basin of River Amur (Stein 1968). It is obvious that the grasscarp and bighead (*Hypophthtalmichthys molitrix*) are not specific hosts for this species (Golemansky and Grupcheva 1975), since *Trichodina nobilis* parasitizes many freshwater fish (Byhovskaya-Pavlovskaya 1964). The total annual infestation of grasscarp and bighead by this species reaches as much as 50% (Golemansky and Grupcheva 1975). This species occurred relatively rarely in our warm fish-ponds where the carp is mainly rared in comparison to Eurasian fish-ponds where mainly herbivore species are reared (Allamuratov 1986). The study of seasonal dynamics of *Trichodina nobilis* showed two maximum values of infestation in Spring and Autumn which points to the fact that this species favours moderate water temperature (7.2-14.8 °C). The explanation of bimodal pattern of seasonal distribution is not yet given, although it is supposed that bimodality occurs due to the better conditions for the fish-pond carp at higher water temperatures (Halmetoja et al. 1992), i.e. due to the stronger immunological response (Aaltonen et al. 1994). The predominance of fish immunological condition over the role of moderate water temperature for infestation by *Trichodina nobilis* could be supposed from the fact that remarkable percentage of infestation occurred also at the warmest months (Figs 2 and 3), when the habitat conditions were less favourable for fish, too.

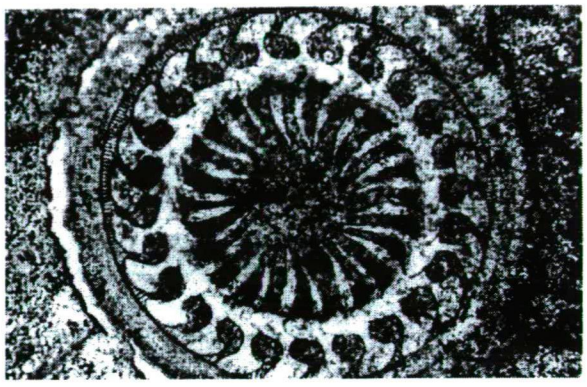

Fig. 3. Oral disk, i.e. the sticking ring of *Trichodina nobilis*, with „cylindrical climbing hooks".

The comparison of infestation rate by *Trichodina nobilis* in the Ečka and Uzdin fish ponds was made between successive months by Kruskall-Wallis H test. This species occurred during the year in different densities, so the values of Kruskal-Wallis test showed very significant differences between successive months in Ečka fish-pond ($H=38.10$; $df=7$; $p<0.001$), but its oscillation was somewhat smaller in the Uzdin fish-pond and also the significant differences decreased ($H=21.00$; $df=6$; $p<0.05$). In addition, *Trichodina nobilis* showed no preference for either mirror or scaled carp during the year (Nikolić et al. 1996).

Acknowledgement

This research work was supported by grant from the Ministrry of Science and Technology of Serbia.

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TISCIA 31, 63-69

AUTUMN HOME RANGE SIZE OF *APODEMUS AGRARIUS* AND SMALL MAMMAL POPULATION DYNAMICS IN THE RODENT ASSEMBLAGE OF A *QUERCO ROBORI-CARPINETUM* FOREST HABITAT

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Horváth, Gy. and Trócsányi, B. (1998): Autumn home range size of *Apodemus agrarius* and small mammal population dynamics in the rodent assemblage of a *Querco robori-Carpinetum* forest habitat. — *Tiscia 31, 63-69.*

Abstract. The population dynamics of a rodent assamblage in a habitat of *Querco robori-Carpinetum* was investigated for three years by means of live trapping on a 1-hectare plot on the Dráva Lowlands. The studied rodent assemblage was made up of four species, with 1007 specimens providing data from a total of 2184 captures. Capture parameters (number of captures, number of recaptures, number of individuals) were the highest in the case of *Apodemus agrarius* (Pallas 1771), especially in 1995 when it dominated the captures in the sampling area in autumn, with significantly higher values in all parameters. The sufficient number of recaptures allowed the calculation of autumn home range size values for *A. agrarius*: for juvenile males in 1994, and for adult males and females in 1995 and 1996. The latter two years had data that were statistically analysable. Males had significantly larger home ranges than females in both years. The comparison of the two years did not reveal difference either in the case of males or females. It was found that calculated home range size in *A. agrarius* was influenced by the combined effect of the number of captures on the one hand and the number of different trap stations visited on the other. Home range characteristics as expressed by the chosen capture parameters were unquestionably influenced by the observed unique population dynamics of *A. agraius*.

Keywords: Apodemus agrarius, *rodent assemblage, population dynamics, home range, minimum convex polygon*

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Introduction

Among the four species (*A. agrarius*, *Clethrionomys glareolus* (Schreber 1780), *Apodemus sylvaticus* (Linnaeus 1758), *Apodemus flavicollis* (Melchior 1834) of the rodent assamblage in our study area, the most studied species from the home range aspect are *C. glareolus* and *A. sylvaticus*. Home range characteristics of *C. glareolus* were investigated by means of live trapping (Mazurkiewicz 1971, 1983). The change in home range size of male and female *C. glareolus* was also analysed as a function of food source fluctuations (Andrzejewski and Mazurkiewicz 1976). Detailed data are available on the relation system of space use, home range and social organization within the population (Ylönen et al. 1988, Mironov 1990, Bujalska 1994). Considerable amounts of information have been published recently about the movement patterns and home range size of *A. sylvaticus*, relying mainly on the radio telemetry method (Wilson et al. 1992, Tew 1992, Tew and Macdonald 1993, 1994, Rogers and Gorman 1995). Knowledge about space use and home range sizes in *A. flavicollis* is more limited (Radda 1969, Wolton and Flowerdew 1985, Kotzageorgis and Mason 1996). Out of the species of the investigated rodent assamblage, *A. agrarius* was captured in the largest numbers, and this species

produced the highest number of recaptures too. This species is less likely to be found inside various forest vegetation types, instead it prefers open habitat types with dense cover, as well as margin and transitional areas (Zejda 1967, Babińska-Werka et al. 1979, Szacki and Liro 1991). Some information have been published about the role of *A. agrarius* in small mammal communities, its space need and movement patterns. Its long distance movements, irrespective of it being dispersal move or sallies around the territory have been investigated. (Liro and Szacki 1987, Szacki and Liro 1991). It had earlier been established regarding small mammal movement patterns that the effective range of movements exceeds the diameter of the home range. (Crawley 1969). However, in order to detect and analyse long distance moves, the trapping grid method is not sufficient, conclude Liro and Szacki (1987) from investigations of *A. agrarius*.

Data on home range size of *A. agrarius* is available from Wierzbowska and Chełkowska (1970), who applied for the species the center of activity method (Hayne 1949), and the home range model based on a two-variable normal distribution catching probability (Calhoun and Casby 1958). The conditions for this type of home range calculations include intensive trapping, large sample size and high population density (Wierzbowska and Chełkowska 1970). It has been shown that effective home range size depends on the vegetation and habitat type, as determined mainly by food availability (Chełkowsa et al. 1985). Similarly, the range of movements, sallies and exploration trips can be dependent on the current state of plant cover and composition that can change with time, and influence, through food offer, population densities. *A. agrarius* populations have been studied in *Tilio-Carpinetum* (Andrzejewski et al. 1978, Chełkowska et al. 1985), and *Carici elongatae-Alnetum* (Andrzejewski et al. 1978, Gliwicz 1981), *Pino-Quercetum* and *Calamagrostio villosae-Pinetum* (Chełkowska et al. 1985).

The present study intends to contribute to the information about the home range characteristics of *A. agrarius* in *Querco robori-Carpinetum* vegetation, with new Hungarian data.

Study area

Our investigations were performed on the Dráva Lowlands in southern Hungary. The sampling grid was laid out on the terrace of Fekete-víz, between the villages Vajszló (N 45° 51', E 18° 00') and Páprád (N 45° 54', E 18° 01') in county Baranya.

The trapped area is a 1 hectare forest section of a *Querco robori-Carpinetum* association, surrounded by low and flat agricultural lands often covered with pools of precipitation.

The most characteristic plant species in the undergrowth are *Dentaria bulbifera, Asperula odorata, Asarum europeum, Primula vulgaris*. Hornbeam (*Carpinus betulus*) is present in the form of young specimens in the second layer of the canopy.

In spring, sections of the sampling area with the densest (90-100%) plant cover are characterised by high undergrowth comprising many weed species and those indicating dampness and soil rich in nitrogene. Characteristic species are *Corydalis cava, Anemone nemoralis, Stellaria holostea, Galium aparine, Veronica hederifolia, Lamium purpureum, Alliaria petiolata, Urtica dioica*. In places of the grid where undergrowth cover is 0-30 %, there is an almost uninterrupted blanket of fallen leaves, and patches of bare ground are also present, with plant species *Ficaria verna, Hedera helix, Ajuga reptans, Crataegus monogyna, Primula vulgaris*.

In autumn, sections with plant cover of 70-90% or as much as 100 %, are characterised with a dense, medium high undergrowth of multiple layers. *Lamium maculatum, Stellaria holostea, Circaea lutetiana, Carex divulsa, Colchicum autumnale, Hedera helix* characterise the herb layer, while the upper layer comprises *Urtica dioica, Solidago gigantea, Dactylis glomerata*, and scattered specimens of *Rubus sp., Tamus communis, Stenactis annua*. Patches with pure blanket of leaves are common in sections with 0-20% cover, with scattered *Circaea lutetiana, Hedera helix, Pulmonaria officinalis, Asperula odorata* specimens. The upper layer has a cover of 60%, made up mainly by small, almost creeping specimens of *Ligustrum vulgare*.

Material and methods

With its 81 box-type live traps laid down in 9 rows at a distance of 12.5 m from each other, the grid covered an area of 1 hectare. Traps operated for three consecutive nigths from March to October 1994 and March to May 1995, then for four nights from June to October 1995 and from February through November 1996. Thus, sampling during the three years yielded a total of 7533 trap nights. Traps were checked twice daily (8^{00} CET and 18^{00} CET). For individual identification of the captured animals, the removal of the first knuckle of certain toes was applied, and the following data were recorded: species, sex (gravidity and lactation in females), body weight.

Capture data were collected in a Manly-Parr diary of captures. Throughout the three years the changes in population sizes in time were monitored using the index "minimum number alive" (= MNA) (Boonstra and Krebs 1978, Boonstra and Rodd 1984) based on capture data. Capture parameters of the different species (i.e. total number of captures, number of recaptures, number of captured individuals, MNA) were compared using the two-sample *t*-test (Zar 1996).

The home range analysis of *A. agrarius* was possible using the autumn trapping data (1994 and 1995: from late August through late October, 1996: from late August till the end of November). Based on data from the three autumn periods, three categories of *A. agrarius* were differentiated: young males in 1994, adult males and females in 1995 and 1996. Individuals captured at least four times and having used a minimum of three traps were included in our calculations. For estimating home rage size, the "minimum convex polygon" (MCP) estimator of the computer programme "McPAAL" (Stüwe 1988) was used. For making comparisons between sizes of home range area of sexes and between those of the 1995 and 1996 autumn trapping periods within the same sex category, the Mann-Whitney *U*-test was applied (Zar 1996). To test a possible correlation of home range size with weight of *A. agrarius* individuals, regression analysis was performed.

Results

Four rodent species were captured during the study period, with the bulk of the captures being made up by specimens of *A. agrarius*, as is indicated by capture, recapture and abundance data in the three years (Fig. 1). A total of 2184 captures denote the following distribution of the four species: *A. agrarius* (AAGR) 405, *A. flavicollis* (AFLA) 284, *A. sylvaticus* (ASYL) 92, *C. glareolus* (CGLA) 226 specimens.

The yearly trends in population changes of the four species are indicated by the MNA values of the three years (Fig. 2).

In 1994 *A. agrarius* was first caught as late as in May, then, together with *A. flavicollis*, it reached an abundance peak by September. According to monthly values of captures, individuals and MNA, *C. glareolus* was found to be significantly more abundant than *A. sylvaticus* (total number of captures: $t = 2.43$, $df = 14$, $p < 0.05$; number of captured individuals: $t = 2.19$, $df = 14$, $p < 0.05$; MNA: $t = 2.81$, $df = 14$, $p < 0.02$). As regards recaptures, there was no significant difference among the four species when the whole year period

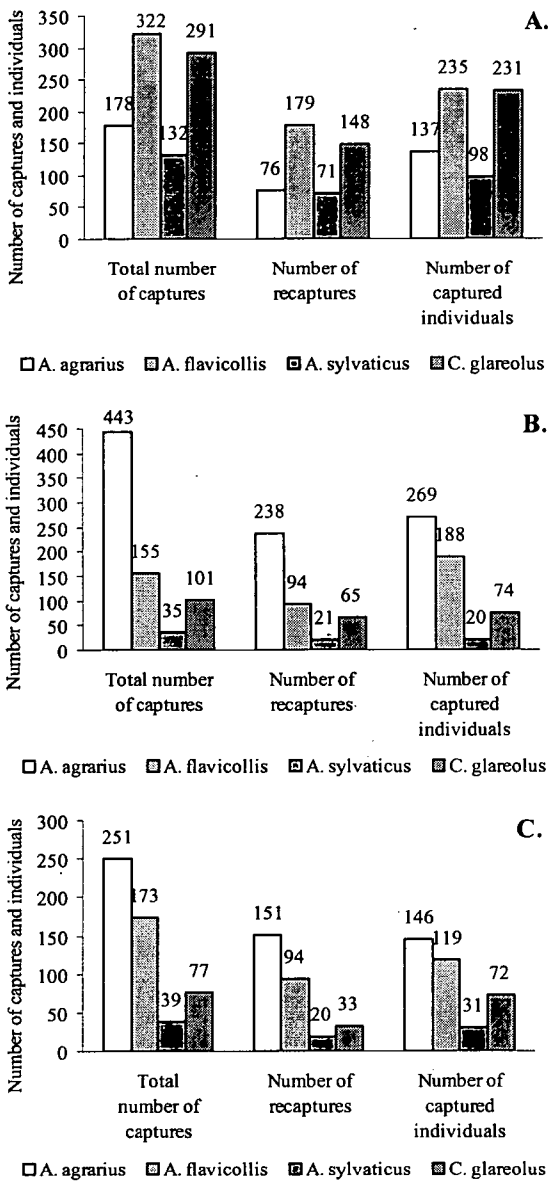

Fig. 1. Captures, recaptures and number of individuals for the four rodent species. A: 1994, B: 1995, C: 1996.

was analysed. The *t*-test of the calculated values was run for the the autumn period in itself, too, which revealed that significantly more indfividuals *of A. flavicollis* were identified than *A. sylvaticus* (number of captured individuals: $t = 4.66$, $df = 4$, $p < 0.01$; MNA: $t = 8.24$, $df = 4$, $p < 0.01$), and, from the aspect of capture numbers and MNA, *A. flavicollis* turned out to be more abundant than *C. glareolus* (total number of captures: $t = 3.72$, $df = 4$, $p < 0.05$;

MNA: $t = 3.05$, $df = 4$, $p < 0.05$). The reason for the latter difference is that in 1994 the population maximum of *C. glareolus* occurred in mid-Summer, unlike in that of the *Apodemus* species.

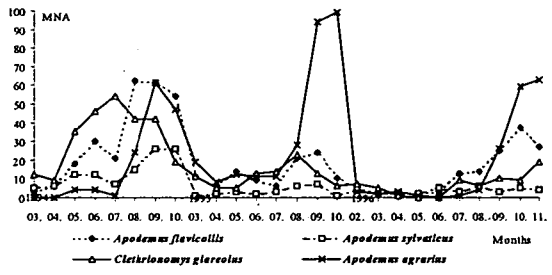

Fig. 2. Minimum number alive values of the species in 1994-1996.

Table 1. Comparison of capture data of *A. sylvaticus* with those of the three other species in 1995. df =14, * $p < 0.01$, ** $p < 0.02$, *** $p < 0.05$.

Species		AAGR	AFLA	CGLA
	Capture parameters		t - values	
ASYL	Total number of captures	2.42***	3.58*	2.82**
	Number of recaptures	2.35***	4.05*	2.89**
	Number of captured individuals	2.4***	3.56*	2.89**
	MNA	2.36***	3.81*	3.55*

The 1995 study period shows an entirely different picture: more *A. agrarius* were captured each month than in the previous year, and its population build-up forming by September-October exceeded by far that in 1994 (Fig. 2). Capture values for the rest of the species suffered a marked decrease. The least abundant was *A. sylvaticus*: each calculated parameter for this species was significantly lower than those of any of the three other rodent species. (Table 1). The striking autumn population growth in *A. agraius* is well demonstrated by its significantly higher number of captures in autumn than any of the other species (AAGR vs. AFLA: $t = 2.87$, $df = 4$, $p < 0.05$; AAGR vs. ASYL: $t = 3.67$, $df = 4$, $p < 0.05$; AAG vs. CGLA: $t = 3.25$, $df = 4$, $p < 0.05$). In the comparison of autumn recaptures, the values for *A. agrarius* were found to be higher only than those of *A. sylvaticus* ($t = 2.85$, $df = 4$, $p < 0.05$), which is attributable to the fact that a considerable proportion of the high number of *A. agrarius* captures in this period was made up by newcomer individuals to the area, and recaptures contributed to the high abundance value only with a relatively low number.

By spring 1996, rodent populations were found to have declined as a result of the long and severe winter of 1995/1996 and the weather in March wich was cold for the season. In the period until August much less animals could be captured than in the same period of the two preceding years, which is well indicated by capture parameters (Figs 1 and 2), and the studied populations could not reach an abundance peak like the one in 1994, not even by September. *A. agrarius*, again, turned out to be the most abundantly trappable species in autumn 1996, but only with a lower maximum than in 1995.

Our data describe a rapid growth of the *A. agraius* population, culminating in autumn, and a subsequent considerable drop in numbers by spring of the following year. This trend was most marked in 1995 with *A. agrarius* becoming by autumn the most frequent species, trapped in highest numbers on the study plot, as is confirmed by data in Tables 2 and 3. When spring and autumn capture data are compared, the *t*-test reveals higher autumn capture values for each year (1994: $t = 4.92$. $df = 6$, $p < 0.01$; 1995: $t = 4.45$, $df = 6$, $p < 0.01$; 1996: $t = 2.83$, $df = 8$, $p < 0.05$). The relatively high number of new individuals trapped in autumn suggests a dispersal of the species from open areas into the forest.

As it is shown by figures appearing together with capture parameters of *A. agrarius* for complete years (Table 2), most of the individuals were captured only once, which characterizes the separate autumn data series (Table 3), too. The rapid population increase in autumn is transparent if figures in these two tables are compared; i.e. figures appearing in the table of autumn data are high percentages of the whole-year figures, showing that most of the captures occurred in autumn. Out of *A. agrarius* individuals captured only once, 96 % , 75 %, and 93 % were caught in autumn in 1994, 1995 and 1996, respectively. Thus, data sufficient for home range calculations are available only from the autumn trapping periods. Table 3 categorises the yearly number of *A. agrarius* individuals captured at two or more different trap stations in the autumn periods. Many individuals were encountered in 2 or 3 different traps, and neither of the known specimens visited more than 5 different stations. In 1994 data of a few young males, while in 1995 and 1996 more specimens both adult males and females were included in the home range size calculations.

MCP values and their staistical evaluations are separated based on these categories (Table 4). Because of the small sample size, the home range data of young males captured in 1994 were not

Table 2. Capture data of *Apodemus agrarius* in the entire trapping period 1994-1996.

Years	Trap nights	Total number of captures	Number of recaptures	Number of captured individuals	Mean number of capt./mouse	Number of mice captured 1-10 times									
						1	2	3	4	5	6	7	8	9	10
1994	1944	178	76	1.37	1.29	53	20	16	9	-	1	-	-	-	-
1995	2349	443	238	269	1.64	101	55	200	18	9	2	2	2	-	1
1996	3240	251	151	146	1.71	32	30	17	15	7	3	1	-	1	1

Table 3. Capture data of *Apodemus agrarius* in the autumn periods.

Years	Trap nights	Total number of captures	Number of recaptures	Number of captured individuals	Mean number of captures/mouse	Mean number of captures/mouse for recaptured mice
1994	729	166	71	128	1.29	2.15
1995	972	355	184	212	1.67	2.13
1996	1296	234	135	136	1.72	2.2

Years	Number of mice captured 1 - 10 times										Number of mice captured at 2 and more different trap stations			
	1	2	3	4	5	6	7	8	9	10	2	3	4	5
1994	51	20	15	8	-	1	-	-	-	-	24	10	3	-
1995	76	48	18	13	8	1	3	1	-	-	51	15	10	2
1996	30	28	18	13	7	3	1	-	-	1	32	24	5	3

Table 4. Home range size of *A. agrarius* in the autumn periods in 1994-1996.

Years	Group (sex and age)	Valid N	Mean of MCP (m^2)	Confid. - 95%	Confid. + 95%	Minimum MCP size	Maximum MCP size	Std. Dev.
1994	Male juv.	4	144	50.45	237.54	72	216	58.78
1995	Male ad.	9	376	215.17	536.82	144	792	209.22
	Female ad.	6	140.97	135.96	143.98	78.125	234	72.53
1996	Male ad.	10	210.95	108.64	313.25	78.128	469	143.01
	Female ad.	7	245.31	52.19	438.42	78.18	703	208.8

included in the statistical comparison of years. First, home range size of adult males and females were compared for autumn 1995, then for autumn 1996. According to the results of the Mann-Whitney *U*-test, adult males had significantly larger home ranges in both years than adult females (1995: $U = 51$, $p < 0.005$; 1996: $U = 51$, $p < 0.05$). However, when the two years are compared, home ranges do not differ significantly either in the case of males or females. (ad. males: $U = 65$, NS; ad. females: $U = 14$, NS).

The regression of home range vs. body weight of the sexes was done separately for the three trapping periods, since the size of the *A. agrarius* population as well as the composition of the rodent community were entirely different in the autumn of the three periods. However, significant correlation was not found in either of the cases. The values of the correlation coefficient were the highest in the case of the 1996 data, obtained for a positive linear correlation for females ($r = 0.446$, $df = 4$, NS), and a negative exponential relationship for males ($r = 0.685$, $df = 4$, NS).

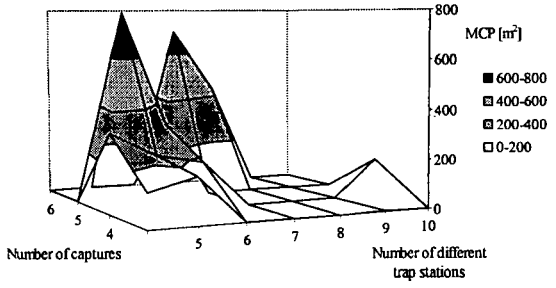

Fig. 3. Calculated MCP size values as a function of number of captures and trap variability. For different individuals with different MCP size values, but with the same number of captures and the same number of visited trap stations, the average of their home range sizes was put on the chart.

Each *A. agrarius* individual that had ben attributed an MCP value was considered when plotting home range sizes against individual capture numbers and number of different trap stations visited (Fig. 3). In the formation of MCP size values, the

use of several different trap stations by the mice has an influential role. However, it was not possible to show a positive correlation between the number of captures and home range size. Out of the pool of *A. agrarius* individuals included in our calculations the highest home range size peak (Fig. 3), was obtained for individuals that were captured 5 times. The other peak occurred in the case of specimens with 6 captures, where the number of trap stations visited was also higher, although it did not exceed the value of the former maximum.

Discussion

In the four-species rodent assablage of the investigated *Querco robori-Carpinetum* habitat the autumn dominance of *A. agrarius* was shown. This species is known from literature (Andrzejewski and Wrocławek 1961) to exhibit abrupt autumn population growths. This yearly cycle was most predominant in 1995 when *A. agrarius* completely had spread in the forest habitat by autumn, and had become trappable throughout the 1-hectare grid, despite its ecoton preference having been described by earlier investigations (Zejda 1967, Babińska-Werka et al. 1979, Szacki and Liro 1991). From the data in autumn 1995, the presence of a gradation was concluded which suffered a drastic collapse by spring 1996. A similar event was covered in a case study by Andrzejewski and Wrocławek (1961).

From our case, the question arises here whether or not the species composition of the studied rodent assamblage and changes in it depend on the size of the actual populations. What kind of relation exists between changes in the structure of the species assemblage and the changes of the structure of co-existing populations? The changes in *A. agrarius* population size in cultivated lands were studied in the presence of *M. arvalis* (Pall.) and *A. flavicollis* (Adamczewska-Andrzejewska et al. 1981). It was found that the increase in the number of mature *A. agrarius* females appeared only at a certain level of density, and showed a decrease beyond a threshold level, while in the case of *M. arvalis* the ratio of mature females grew steadily following the pace at which the size of the population increased, and reproduction followed a linear growth. As opposed to *A. agrarius*, there is no negative feedback from density on reproduction in *M. arvalis*. When the *A. agrarius* population co-existing with *C. glareolus* was removed, Bujalska and Janion (1981) recorded an increase in the number of reproductive *C. glareolus* females, meaning that a change in the structure of the community was followed by a shift in the structure of the *C. glareolus* population.

Our results showed that population sizes in the rodent assamblage were different in the three study years. The autumn increse in the densities of the populations also differed from species to species. In 1995 *A. agrarius* was predominant in comparison with the rest of the species. The home range size values of either male or female *A. agrarius* were not different when 1995 and 1996 were compared. From these we can conclude that in forming home range sizes characteristic for males and females respectively, the role of interactions between different populations was rather insignificant.

The home range size of rodents is determined by a composite of almost innumerable factors the separate identification of which is extremely problematic. Examples showed that home range size decreases as a function of increasing plant cover (e.g. Getz 1961), and, similarly, smaller home ranges are revealed when density increases (Van Vleck 1969) or the amount of available food is greater (Andrzejewski and Mazurkiewicz 1976). Besides, behavioural characteristics of various functional groups of a population may have an influential role in forming certain home range variations (Korn 1986). From his results Korn (1986) concluded that average values in the case of home range can be misleading, therefore suggests that as many functional groups of individuals be differentiated as possible instead of using mean values, so as to be able to correctly interpret the observed phenomena. Similarly, it can be deceiving if averages from the data of a longer time period are created unconditionally in home range calculations, since temporal intervals defining actual home ranges can be in some cases as short as only a few hours (Mironov 1990). Bearing in mind the suggestions mentioned above, age and sex categories were differentiated in the present study, and time intervals were separated. For autumn 1995 and 1996, it was possible to use data of only adult males and females. *A. agrarius* males had significantly larger home ranges than females. In accordance with these findings, when examining territoriality of *C. glareolus* males and females (Bujalska 1994), and in the study of the same species and *A. sylvaticus* (Korn 1986) it was found that females had smaller home ranges than males. Unfortunately, since we had calculations based on only one period in both years, it was not possible to obtain statistically comparable home range overlap data.

One autumn period in each year of the investigations can not provide sufficient data to answer how much the variations in the home range size of *A. agarius* depend on factors like vegetation cover, population density and food availability. To

reveal these, much more capture data are needed. However, even in the case of a very intensive capture programme operating with more traps, the results can be seriously influenced by the unpredictable population dynamics of *A. agrarius*.

Acknovledgements

This project was supported by National scientific Research Grant (OTKA No. F 021184).

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TISCIA 31, 71-84

INFOTHEM PROGRAM: NEW POSSIBILITIES OF SPATIAL SERIES ANALYSIS BASED ON INFORMATION THEORY METHODS

A. Horváth

Horváth, A. (1998): INFOTHEM program: new possibilities of spatial series analysis based on information theory methods. — *Tiscia 31, 71-84.*

Abstract: The aim of the INFOTHEM 1.0 program is to analyze coenological patterns based on information theory models in a spatial series approach. The analysis, concept of which was developed by Juhász-Nagy, was applied to describe coexistence structures of vegetation. The facilities of program include numerous functions of both syncretic and diacretic models. It is also possible to use Rényi's general entropy formula rather than Shannon's formula. The spatial scaling of information theory functions is integral part of program operation, so there are some procedures to organize fusion of primary sampling units in steps of the spatial series. For the statistical evaluation, to estimate deviation from null hypothesis, the program is able to generate many types of random patterns considering different random references, and to calculate the significance levels using Monte-Carlo simulation. The features and operation of the program are discussed with some remarks on the application of information theory models.

Keywords: coexistence structures, information theory models, loess grasslands, random reference, spatial series analysis

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Introduction

The analysis of coexistence structures of vegetation was developed by Juhász-Nagy (1967, 1972a, 1972b, 1973, 1976, 1980a, 1980b, 1984, 1985) on the basis of information theory mainly in the sixties and seventies. The theory concentrates upon the most cardinal question of plant community research: is there any spatial dependence of populations existing in a given stand (Juhász-Nagy 1976, 1984)? In contrast to traditional approaches focusing only on the pairwise association between species, Juhász-Nagy's methods apply to the entire community (associatum as total association, Juhász-Nagy 1967, 1972a). Since the pioneer works by Juhász-Nagy, a new measure, the so-called mean compositional information (Podani and Czárán 1997) has been developed as a connecting link between the individualistic approach and the investigation of coexistence structures.

The information theory methods represent a unique tool to describe the coexistence structures of multispecies pattern (cf. Podani *et al.* 1993; Podani and Czárán 1997), by placing the basic coenological phenomena (preference, diversity and resemblance) into a coherent framework (Juhász-Nagy 1986). Information theoretical functions are additive, well-manageable and programmable. The spatial scaling is inherent and essential part of the models, which use the concept of characteristic areas in a more comprehensive sense than minimum area (Juhász-Nagy and Podani 1983). Consequently, the problem can only be approached by spatial series sampling (spatial process: Podani 1984a, space series: Podani 1992, spatial series: Erdei and Tóthmérész 1993). Finally, the models give possibility to study the spatial pattern on both community and population levels (syncretic and diacretic models: Juhász-Nagy, 1973, 1980a), even reflecting to coalitions.

Although the fundamentals were developed more than twenty years ago, and the test of models started at that time, too, extensive applications could not begin until computers were available (due to the many calculations, cf. Erdei *et al.* 1994). The first published analyses (e.g. Juhász-Nagy and Podani 1983) were calculated with the SYN-TAX program

package (Podani 1980, 1988). Other computer programs have been made since then, such as MULTIPATTERN (Erdei and Tóthmérész 1993; Tóthmérész and Erdei 1995), and JNP-MODELLEK (Bartha *et al.* 1994). There were several field studies using the full capabilities offered by the programs. These suggest some new methodical and methodological problems which did not arise earlier. One of these problems is the question of primary sampling (e.g. planning of the sampling area and arrangement of sampling units in the field), another is the problem of spatial scaling (in fact: execution of secondary sampling by fusion of primary sampling units, that is the organization of spatial series steps usually by the computer, see below). The next problem is the question of random references and significance tests, and finally the role of rare species (cf. Tóthmérész and Erdei 1992) should be mentioned.

In this study the first three problems are surveyed. In addition to these theoretical problems, there is one more requirement in practical computer work, namely the well-structured, arranged and transportable files of results. The INFOTHEM program has been developed with this in mind, in IBM DOS compatible environment. First the methodical problems are discussed (summarizing the known possibilities and proposing the new procedures), then the use of the program is explained. As an example we illustrate the results of own field data collected in several types of loess plant community from Mezőföld region.

Methodical comments

Primary sampling

Sampling experiments for testing the information theory methods were carried out based on theoretical considerations (Juhász-Nagy 1972a). In this way there are several sampling sets corresponding to specified spatial series steps, and each set contains a certain number of sampling units of a given size. The shape of sampling units is, for example, circular and plots are located at random in the study area (Juhász-Nagy 1980a; Juhász-Nagy and Podani 1983). Thus, spatial scaling was realized directly in the field. If all plots are located separately and randomly, we can speak about *independent plots*, whereas the *nested plots* mean that we laid down first the plots belonging to the largest area set, and these units will completely include plots of other smaller sets (Podani 1984a). Usually we use isodiametric units of any shape (circular or square especially, cf. Juhász-Nagy and Podani 1983; Podani *et al.* 1993).

Since a large number of sample plots is necessary for the analysis in each steps of the spatial series, the above sampling technique requires exhaustive field work. To reduce sampling effort, we can use a *grid* or a *transect*, in which the plots are in contact with each other by their four or two sides. (A *map* can be considered as a grid consisting of infinitely small units, namely continuous X, Y coordinates.) In this case the spatial scaling will be realized after field sampling in the *secondary sampling*.

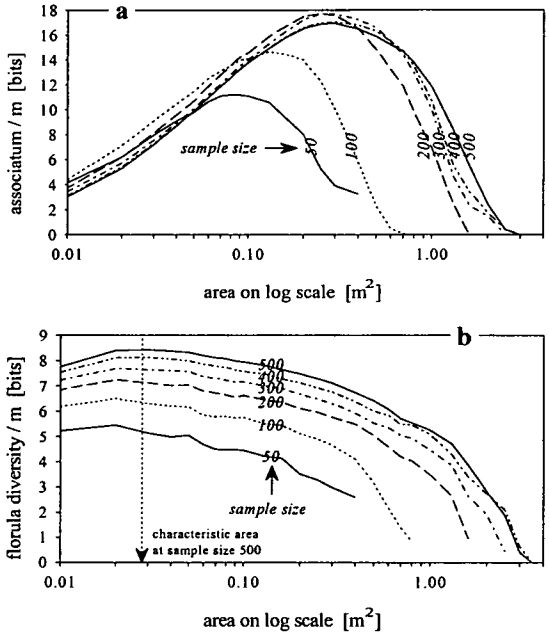

Fig. 1. The effects of unit size and sample size on the characteristic functions. If sample size is too small (in this case less than about 300), both the maximum value and area of maximum value is translocated, so the curve of associatum becomes deformed (**a**). We can see on diagram **b**, that using larger than 0.03 m^2 unit size we lose the real global maximum value of florula diversity curve, and the characteristic scaling is false or is not possible. The data result from a loess grassland community consisting of 31 species with more than 1% relative frequncies.

When we plan the field (primary) sampling, we have to choose either a grid or a long transect, and define primary unit size, and the number of units (sample size). *Sample size* depends on the number, composition and association of species; the empirical ratio of the number of units and species is at least 5-10 (e.g. 200/8=25 in the *Saxifraga stellaris* coenotaxon [Juhász-Nagy 1980a], 2500/37=68 in a steppe community [Bartha and Horváth 1987], between 2750/3=917 and 2750/21=393 in primary succession [Bartha 1992]). If sample size is too

small, the shape of the characteristic functions can become distorted, and characteristic scaling will be imperfect (Fig. 1a). *Unit size* depends also on composition of species; in a diverse, intact grassland it is about 25-100 cm^2 (e.g. 5×5 cm in dolomite grassland communities [Szollát and Bartha 1991], 10×10 cm in loess grassland [Bartha and Horváth 1987], 20×20 cm in pioneer communities [Bartha 1992]). If unit size is too large, the characteristic areas can be outside of the surveyed spatial scale (see Fig. 1b). To choose between grid and transect, we consider two aspects. The long transect (consisting of the same number of units as a grid) spans a larger area of the stand, and yields less redundant data. On the other hand, when applying a long transect, influence of elongated secondary sampling unit must be considered (see Nosek 1976; Podani 1984a, 1984b; Bartha and Horváth 1987 for more details).

Secondary sampling

Secondary sampling is unavoidable for spatial scaling if a grid (or transect) is used to collect data. (For mapped point patterns of species, the secondary sampling usually involves circular plots [cf. Podani 1984b; Podani and Czárán 1997].) Primary plots will be fused in a predetermined arrangement, producing *secondary sampling units*. Fusion means that in the secondary unit a species is present, if it occurs in any primary unit fused, in other words logical "or" operation will be performed among binary values of primary plots. In each step a certain number of primary plots are fused, in a regular manner. This means that the units to be fused must be contiguous. The shape of secondary unit is usually isodiametric in case of grids, and elongated in case of transects. (Sometimes we merge units that are positioned in the grid randomly; this is a procedure to make a type of random references.) There are two important alternatives to define secondary plots on a grid: randomly (*random sampling*) or regularly (*systematic sampling*). In random sampling we use a constant number of plots in each spatial series step. In this case all area of the grid is sampled more or less uniformly (except edges) supposing that sample size is sufficiently large. Using systematic sampling we have to shift units on the grid by a given number of primary units. This number differs from each other with the size of secondary plots. In this case we must guarantee (by programming appropriate offset) that the complete area will be sampled uniformly. If the offset is only one primary unit long, we have the so-called *complete sampling* (cf. Bartha *et al.* 1995), since the grid is completely sampled from all possible positions in all spatial series steps. In case of complete sampling, the number of secondary units varies in the different spatial series steps, so it must be standardized with sample size.

Although the first analyses were executed with random secondary sampling, it can be shown that the curve fitted to values of any information statistical function depending on sample size reaches the expected value in the infinite, whereas complete sampling gives good approximation (see Fig. 2). The explanation is that in complete sampling plots are located to all possible place exactly once. Because it is the computer program that performs secondary sampling, complete sampling is easily accomplished, so that standardization with sample size is always performed.

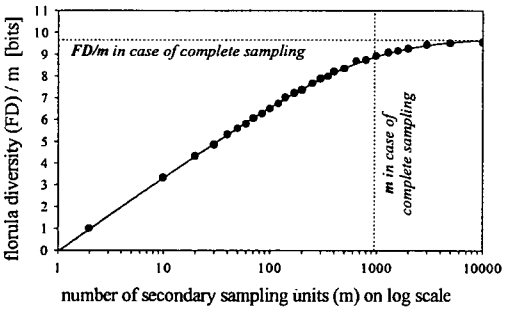

Fig. 2. Comparison of random and complete sampling for standardized florula diversity. Field sampling was made in a loess grassland community, using a 50×25 grid of 20×20 cm units. The size of the secondary sampling unit is 1×1 m. Applying random sampling the equation of curve (solid line) fitted to empirical values (points): $y=9.75+3.38\log(x/x+790)$, so the expected value in infinite: 9.75 (correlation coefficient of fitting: 0.9998). At sample size (m) 10000 we get 9.56 that is the nearest to the expected value. Using complete sampling, this value (exactly 9.63) results at m=966 (dotted lines).

For the spatial series the determination of the size of secondary units is needed. The increment of size along the spatial scale depends on the requested accuracy of measures; fine resolution of scale is important near characteristic areas (which are unknown before analysis). Usually we use a logarithmic spatial scale, so the increment will cause the exponential enlargement of the secondary unit. To determine the area of the largest secondary unit we must consider that its area must be smaller than about the quarter of total sampling area (because of the edge effect).

Random references

Studying the coexistence structures of communities, we expect that there is spatial dependence (pairwise and multiple) among species. So, our null

hypothesis is that populations living in a stand are completely independent from one another (cf. metamethodological quadruplet: Juhász-Nagy 1986). This means that they are combined randomly with each other at all spatial scales. Therefore, to prove the existence of coexistence structures (patterns), we have to use significance tests to show the difference from randomly combined species. There are some problems regarding the hypothesis test of associatum and other functions. First of all, larger than zero associatum does not necessarily represent real spatial dependence because of the textural and structural constraints derived from the abundance and spatial pattern of species (see Podani 1982, 1984b; Szollát and Bartha 1991; Bartha 1992; Tóthmérész and Erdei 1992). Secondly, if secondary sampling units overlap, namely some regions of the study area may take part in many sample plots, the studied area is "over sampled" (this is valid in most cases), and thus the criterion of independently placed sample plots does not satisfy, therefore conventional significance tests do not apply (Podani 1984; Podani *et al.* 1993). Thirdly, conventional significance tests have not been developed for information theory methods, because there is a multitude of parameters of species (abundance, dispersion type) which should be considered for the null model. (We can produce random references by direct calculation of florula frequencies assuming the Poisson distribution for all species; cf. Podani *et al.* 1993; Erdei *et al.* 1994; Podani and Czárán 1997.) Usually there is only one possibility: to compare the functions derived from field data to *random references*, and to use *Monte-Carlo simulations* as a basis of the significance test.

Considering different null models, there are several *types of random references*. In any case, we transform one or more parameters of the population or pattern into random. Table 1 shows some types (marked with numbers and names) according to unchanged or altered (random) parameters. (The role of variable called "RRType" (Random Reference Type) will be detailed later.) In case of first type we randomize the location of the primary sampling units in a grid. In case of types 2–4 we relocate species occurrences in a grid, so the species will combine randomly. In case of the fourth type only species frequencies will be constant; this is the so-called *complete randomization* (Bartha 1990, 1992; Tóthmérész 1994b; Bartha *et al.* 1995; Margóczi 1995). In case of the third type the distribution of species number in sampling units will also be held constant, while in the second type, in addition, the species number of each plots in the given position of sampling area will be unchanged. In the types 5–8 the species frequencies are fitted to a certain species-abundance distribution model, and species are mixed randomly.

If we want to preserve species distribution type (pattern) in space, we must choose the ninth type of random references (see Table 1). In this case we shift the pattern (the patches) of a species along two dimensions of grid, or alongside transect by randomly generated number of primary units (Fig. 3a-b). This process does not change the distribution of species if we have circular transect, because the opposite ends of ring-shaped transect are connected (Fig. 3c). Now, the random shift occurs as a random rotation. This sampling design is introduced as "trainsect" (Palmer and van der Maarel 1995), and its application is detailed by Bartha and Kertész

Table 1. Types of random references. Symbol ≡ shows if a parameter agrees with the value in the original pattern. See text for more details.

Name of the random reference	*Number of type (RRType)*	*Frequncy of species*	*Distribution of species number in plots*	*Distribution of species number in space*	*Species combination in plots*	*Pattern of distribution of species*
plot randomization	1	≡	≡	random	≡	random
	2	≡	≡	≡	random	random
	3	≡	≡	random	random	random
complete randomization	4	≡	random	random	random	random
making of random patterns with species frequencies deriving from some species-abundance models	5	random	random	random	random	random
	6	geometric distribution model	random	random	random	random
	7	linear distribution model	random	random	random	random
	8	broken stick distribution model	random	random	random	random
random shift	9	≡	random	random	random	≡

(1997). Although in grid or transect the edge effect appears (patches of aggregated species will be separated or fused, see Fig. 3a-b), if patches are not too big compared to sampling area, and there are many patches, this method will more or less preserve the original distribution of species. Since shift length varies randomly with different species, populations will be combined randomly. We can generate patterns of multispecies community with the MULTIPATTERN program package (Erdei and Tóthmérész 1993), supposing that we know all species parameters.

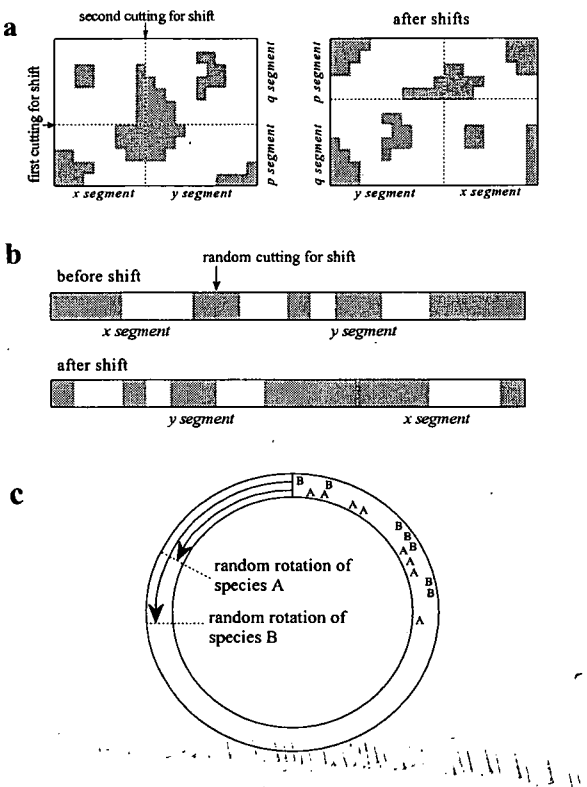

Fig. 3. The possibilities of random shift to generate random references in several types of sampling arrangement. In **a** and **b** the dark patches indicate the pattern of a species, while in **c** two populations (A and B) occur along just the quarter part of circular transect together or separately. In case of a grid two random shifts are needed at right angles to each other (**a**), and only one in case of transect (**b**). In the circular transect the random shift appears as random rotation (**c**). The **c** diagram shows that the lengths of shifts may differ by species, so the original species combination will be converted into random.

Because different random references indicate different null models, the evaluation of results has to consider the transformed and unchanged parameters of original pattern. The random shift (type 9) represents the strongest limitations for randomization, so the differences between the values of field and random data are probably the smallest in this case. The preservation of distribution of species number in sampling units is also relatively strong limitation (types 1–3), in absence of it (but not changing the species frequencies: type 4), we have less defined random references. Among the other listed types (5–8), that type is the nearest to the field situation which contains the most fittable species–abundance model to original frequency distribution. On Fig. 4 we can see an example to study the results applying the different types.

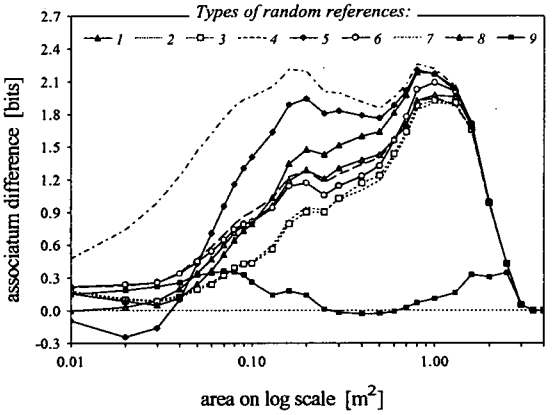

Fig. 4. Curves of differences between associatum values derived from field data and several types of random patterns. Data of 500 primary units originate from a pioneer loess plant community, species number is 11 (without rare species). We have 29 random references at all types, and perform complete sampling. In all cases we can detect positive differences in nearly the total interval of the spatial scale, so the organization in pattern of community has been demonstrated. The level of difference refers to distance between the null model and the field situation. For example, the curve of type 8 (broken stick distribution) has higher values than curve of type 6 (geometric distribution), which confirms that the species-abundance relation represents an initial stage in the succession of communities.

For significance test we apply a Monte-Carlo simulation (cf. Galiano *et al.* 1987; Bartha 1992; Podani *et al.* 1993; Bartha *et al.* 1995; Podani and Czárán 1997). We make many random patterns of a given type of random references, and analyze them with the same method used for the field data. The simulated values determine a random envelope along the spatial scale. If the original curve runs inside the envelope the field pattern probably does not differ from random patterns (cf. Fig. 5a). To calculate significance level, in case of each random pattern we examine whether the original value is under or above (or equal to) the random value. We do not have predetermined hypothesis in case of a concrete function, so if the number of positive differences is

higher than the number of negative differences, the hypothesis is that we have a larger value than which derive from the random reference; and vice versa.

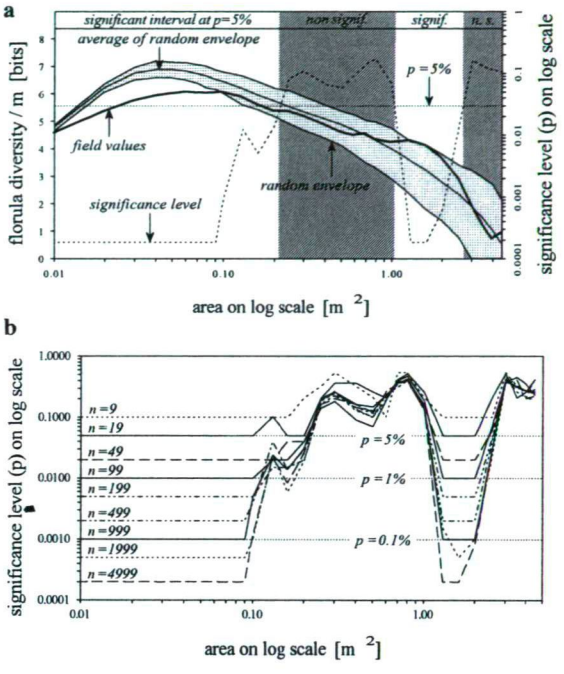

Fig. 5. An example to evaluate the florula diversity curves of random references refering to the significance levels. The diagrams were calculated from the data of a pioneer loess plant community, species number was 18. We use the type 4 for the randomization. The number of random references was 4999 in case of **a**, while in **b** we have a set of different numbers (n). In **a** we can see two significant (non shaded areas) and two non significant (shaded areas) spatial scale intervals at p=5%. The **b** diagram shows that this intervals do not vary with n, if n is greater than 19 (the curves cross the pointed line of p=5% level at approximately same locations). Reducing the number of random references there are three results: (1) in significant intervals p increases, but it remains inside the accettable domain (if n is not too low!), (2) in non significant intervals p keeps its high and more or less constant, non-accettable value, (3) in transitional interval (now: $0.1m^2<area<0.2m^2$) p seems to be partly unpredictable (varies between about 1% and 5%). Of course, increasing n, the reliability of statistical measure increases also.

The level of significance, p (probability of type I error) is given by:

$$p = \frac{n - ND + 1}{n + 1}$$

where n is the number of randomizations, ND is the number of positive or negative (the higher) differences between field and random values. (For example, if we have 99 random references, and the number of positive differences is 3, number of negative differences is 95, and there is no difference in one case, the actual hypothesis is that field value is lower than the random, and

$$p = [99 - 95 + 1]/[99 + 1] = 0.05.)$$

It is necessary to take numerous random references to produce an acceptable significance level, while considering the available time for calculations (cf. Fig. 5b).

The incidental effects of rare species appear mainly with random references, causing a widening of random envelope at larger values of spatial scale

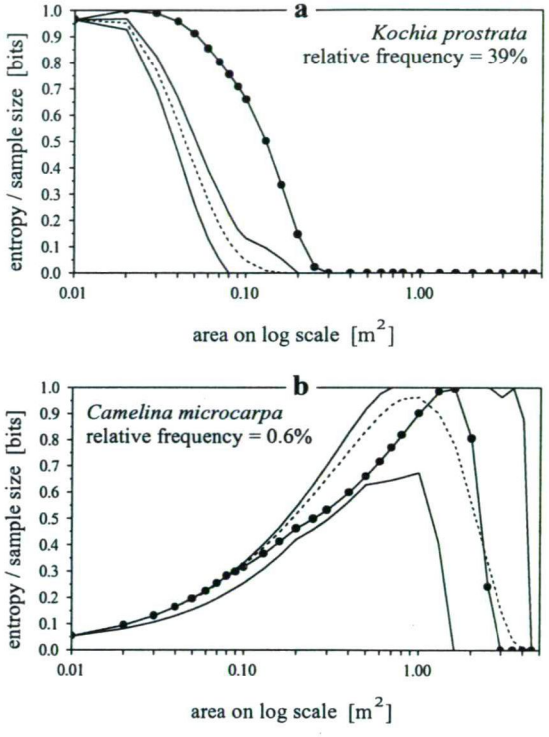

Fig. 6. Entropy curves of two species with different frequency from a pioneer loess community. The number of primary plots is 500, and complete sampling was performed using 99 random references. The line with full circles represents the curve derived from field data, the solid lines indicate the maximum and minimum values of random references; and the dotted line is the average of them. In case of high frequency the random envelope is narrow (**a**), while for very small frequency it becomes wider in which the field values are found (**b**). This means that the concrete location of a rare species has strong, but vagueness-increasing influence on entropy curves. Because the local distinctiveness is the sum of entropies, rare species could produce disadvantageous effect in information theory functions.

(Podani *et al.* 1993). It can be seen in Fig. 6 that in case of a frequent and aggregated species the entropy curve is shifted right from the random reference, but the entropy curve of a rare species has a wide random envelope along the whole spatial scale.

Therefore it could be necessary to neglect rare species with relative frequency less than about 1% (cf. Bartha and Horváth 1987; Bartha 1992; Tóthmérész and Erdei 1992). Tóthmérész suggests to solve the problem of rare species using Rényi's general entropy functions (Tóthmérész 1994a).

Table 2. Formulae to calculate the required memory capacity for the program. The meaning of the variables can be found in Table 4. *Notes:* (1): If every parameter has its maximum value; (2): If QN=maxQO=1000, PN=50, NSP=25.

Necessary result	*Output file extension*	*Memory requirement (bytes)*	*Maximum required memory (1)*	*An example of required memory (2)*
synchretic values	RSA	QN · 25 + max QO · 50 + NSP · 30	753 kB	75.75 kB
diachretic values	RSB	max QO · 25 + PN · NSP · 30	850 kB	62.5 kB
Rényi's entropy	RSC	NSP · 738	73.8 kB	18.45 kB
pairwise association	RSD			
lists of florulas	RSE			
If random references are needed:		QN · 25	250 kB	25 kB
• synchretic values	RSF	NSP · 90	9 kB	2.25 kB
• diachretic values	RSG	PN · NSP · 66	1.32 MB	82.5 kB
• pairwise association	RSH	PN · PN · NSP · 14	56 MB	875 kB
		sum total:	60 MB	1.14 MB

Description of INFOTHEM 1.0 program

General specifications

The INFOTHEM program has been developed by reflecting the methodical problems detailed above. The most important new facilities are that the program can realize various types of the secondary sampling procedures and random references, calculates the significance level for randomizations, and creates well structured output files.

The program is a DOS application, so it can be started in most user interfaces (e.g. DOS, Norton or Windows environment) on IBM PC-s and compatible machines. Because calculations may be time consuming for a big data matrix, a fast computer with numerical coprocessor and about 8 MB RAM can be useful. To count the required memory capacity we can refer to Table 2. If capacity is not enough (the program aborts), we have two possibilities: (1) to quit the „shell" program which uses much memory (e.g. Windows), and to work in plain DOS environment; (2) to get the different output (result) files one by one (this is realizable by setting the Res parameter in the parameter file; see Table 3).

A data file and a parameter file are necessary for running the program. The type of all files (output files also) is *text file* (ASCII-file). The input (data) file is just like a data matrix with sampling units as rows and species as columns. The values may be binary (presence/absence) or quantitative abundance (frequency), but the program transforms all data types into binary. At least one space or tabulator character has to separate each value, the number of delimiters is not fixed. If the sampling area (grid) consists of m rows and n columns, the units are given row after row in the matrix.

The parameter file consists of at least six rows. The first five rows contain the general parameters for program running and analysis; the parameters of every spatial series step are specified in the next one or more rows (Table 3). Therefore, the number of rows in the parameter file is the number of spatial series steps plus five. The meanings and limits of parameters are given in Table 4, and Fig. 7 gives an example for parameter file structure. If the parameters are not adequate, the program aborts. We can make the parameter file directly using any editor program (e.g. DOS or Norton Editor), or interactively by the program. If we have a parameter file ready, we can start the program by entering the name of the parameter file after the program name.

Table 3. The structure of the parameter file. The content of sixth rows is repeated for each step of the spatial series.

row 1	FI
row 2	FO
row 3	QN PN
row 4	FType QS RN NSP Res
row 5	RRType RRNumb MaxFr MinFr
row 6	Area QO QR RF SH BR BD

Table 4. The description and limits of parameters.

parameter	*description*	*notes*
FI	name of input (data) file	with path, if necessary
FO	name of output (result) files	without extension!
QN	number of plots in data file	$1 < QN \leq 10000$
PN	number of species (populations)	$1 < PN \leq 200$
FType	type of fusion of primary sampling units for secondary sampling	=1: random, plot-repeated fusion =2: random, non-repeated fusion =3: regular fusion, systematic sampling =4: regular fusion, random sampling
QS	number of plots in one row of grid	in the sampling area
RN	number of rows of grid	in the sampling area
NSP	number of spatial series steps	$1 \leq NSP \leq 100$
Res	code to set the required output (result) files	serial number of character of an output file type: RSA(RSF)=1, RSB(RSG)=2, RSC=3, RSD(RSH)=4, RSE=5 (e.g. Res=11010)
RRType	type of random references	=0 ... 9 (see Table 1 for more details)
RRNumb	number of random references	$1 \leq RRNumb \leq 10000$
MaxFr	frequency of the most frequent species	$1 \leq MaxFr \leq QN$
MinFr	frequency of the rarest species	$1 \leq MinFr \leq QN$
Area	area of a secondary plot	decimal number is allowed
QO	number of secondary plots	$1 \leq QO \leq 10000$
QR	width of a secondary plot	in number of unit of primary plots
RF	height of a secondary plot	in number of unit of primary plots; $1 \leq QR \cdot RF \leq 10000$
SH	length of shift	in number of unit of primary plots
BR	number of shift to skip	see text for more details
BD	length of skip	in number of unit of primary plots

While the program is running, screen displays the name and extension of required output files under the heading, and in the next four rows the number of steps left. The program will finish the analysis when each value becomes zero.

```
DATA.DAT
RESULTS
25 6
3 5 5 3 11111
4 99 1 1
0.01 25 1 1 1 1 0
0.02 20 2 1 1 4 1
0.04 16 2 2 1 4 1
```

Fig. 7. The contents of the example parameter file named PAR.

Setting of parameter values

In one row of the data (input) file the values of all species follow one another. The maximum number of species is 200, and we can set it by PN parameter in the third row of parameter file (see Table 3). The QN parameter represents the number of primary sampling units; its maximum value is 10000. For grids the value of QS (number of plots in one row of grid) and RN (number of rows) is more than 1, but in case of a transect RN=1.

The name of the input file with extension and path is entered in the first row of parameter file. The second row contains the name of the output file without extension, because the extensions will be attached by the program according to the required results. The meaning of different extensions and the roles of output files belonging to each extension are given in the first two columns of Table 2, but the details will be explained below. The required results (selected types of analysis) can be determined by the Res parameter. This parameter consists of five characters referring to the first five output files (with extensions RSA, RSB, RSC, RSD and RSE). If a given character of Res is 1, the given output file is necessary, otherwise it is 0.

The secondary sampling type is set by the FType parameter (cf. Table 4). FType controls the arrangement of primary plots for fusion. The fused plots form the secondary unit. The fusion may be of four kinds. If FType =1, the positions of plots for fusion are random in the grid, and some plots may be fused again many times. In case of FType =2, the difference is that now a plot can be fused only once, so the maximum number of secondary units comes from QN/QO. These two values of FType give possibility to make two types of random references. However, if we want to compare values of a model

derived from field data to random references, we have to choose other options as given below. In the case of FType =3 or 4, systematic or random secondary sampling will be performed using regularly shaped secondary plots.

The value of the NSP parameter equals to the number of steps in the spatial series. The parameters of each step succeed row by row in the parameter file started at the sixth row. The Area (area of secondary sampling unit, actually the identifier of a given step) is the only informative parameter for the user, the program does not calculate with it, but it will be listed in the output files. QO determines the number of secondary plots in a given step; QO=QR·RF. The dimension of a secondary unit is given by the QR and RF parameters, similarly QS and RN specify the dimensions of sampling area. QR and RF have meaning only if FType=3 or 4, otherwise their product is important. If we have a transect, RF=1.

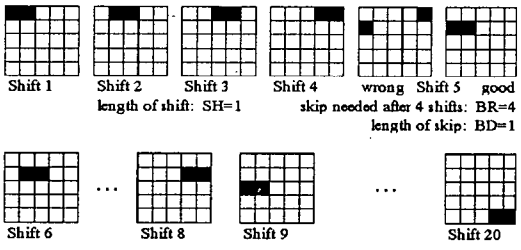

Fig. 8. Demonstration to set parameters of the systematic secondary sampling according to the second spatial series step listed in seventh row in parameter file in Fig. 7.

The SH, BR and BD parameters are larger than zero only in case of systematic sampling (Ftype=3). SH indicates the length of shift on the grid by a given number of primary units. In complete sampling SH=1. If we work on a grid, and the dimension of the secondary unit is larger than 1×1 primary plots, it has to perform skip when the secondary plot reaches the margin of grid. The length of skip is given by BD, and the number of shifts before each skip is given by BR. Fig. 8 explains the meaning of these parameters. To design spatial series steps using visual control, the determination of parameters can be performed by the SPATPROC program developed by the author. If we adopt complete sampling, the preparation of the parameter file is recommended by the INFOTHEM program (started without parameters), because the program will calculate the SH, BR, BD parameters in all steps of the spatial series.

When random references are not needed, the value of RRType is set to zero, otherwise it falls between 1 and 9. The different types of random references are listed in Table 1 (see also "Random references"). If species frequencies are fitted to species abundance models (RRType=5–8), the value of MaxFr is equivalent to the frequency of the most frequent species, and MinFr indicates the frequency of the rarest species, otherwise their value is zero. The number of random references is adjusted by the RRNumb parameter. If RRType>0, then files with RSF, RSG and RSH extension will be output, if RSA, RSB and RSD output files are needed (cf. setting the Res parameter).

The output files

There are five output files for the results, and another three for the versions of random references (cf. the first and second columns of Table 2). The output files are standard ASCII-(text) files, and their data are well arranged and structured, so it can be easily transported to any graph or chart editor program (e.g. Excel 5.0). The first seven rows of each output file are constant, they contain the general parameters of the analysis (cf. Fig. 9). The files with random references have additional three rows (e.g. Fig. 10).

```
Name of input file: DATA.DAT
Name of parameter file: PAR
Number of quadrat in input file: 25
Number of species: 6
Dimension of sampling area: 5*5
Type of quadrat fusion: 3
Number of spatial process steps: 3

  Area    QO  QR  RF  SH  BR  BD    FDiv     FEv     LD      LEv    Ass
-------------------------------------------------------------------------
0.01000   25   1   1   1   1   0   102.59  0.88363  143.42  0.95612  40.83
0.02000   20   2   1   1   4   1    70.93  0.82057   88.91  0.74094  17.98
0.04000   16   2   2   1   4   1    26.03  0.40665   30.63  0.31906   4.60
```

Fig. 9. A detail from the RESULTS.RSA sample output file.

The function of the RSA output file is to store the values of the most common syncretic models. The designation, meaning and formula of these models are found in Table 5. The source of variables and formulae used is Juhász-Nagy, 1976, 1984, 1985 and Juhász-Nagy and Podani, 1983. In the file the results of each single spatial series step follow row by row after the heading. The width of rows is 354 characters. An example can be found in Fig. 9.

Table 5. The variables listed in the RSA file. ST=standardized by number of plots. The basic variables: m=number of plots, s=number of species, i=a given species (i=1..s), j=a given step of the spatial series, k=a given species combination (florula), f=frequency of a species combination, g=a given plot (g=1..m), n=frequency of a species.

designation	*description and formula*
FDiv	florula diversity: $mH_j^{(\varphi)} = m\log m - \sum_k f_{jk}\log f_{jk}$
FEv	florula evenness: $mV_j^{(\varphi)} = mH_j^{(\varphi)} / (m\log m)$
LD	local distinctiveness: $mH_j([L]) = sm\log m - \sum_i \left[n_{ij}\log n_{ij} + (m-n_{ij})\log(m-n_{ij})\right]$
LEv	relative local distinctiveness: $mH_j([L])/sm$
Ass	associatum: $mI_j(\lambda) = mH_j([L]) - mH_j^{(\varphi)}$
Com	number of realized species combinations: ω
FDiv/Q	ST florula diversity: $H_j^{(\varphi)}$
Ld/Q	ST local distinctiveness: $H_j([L])$
Ass/Q	ST associatum: $I_j(\lambda)$
Com/Q	ST number of realized species combinations: ω/m
ESV	entropy of species valences: $N_jH_j(V_q) = N_j\log N_j - \sum_i n_{ij}\log n_{ij}$
ESI	entropy of species invalences: $n_jH_j(v_q) = n_j\log n_j - \sum_i \left[(m-n_{ij})\log(m-n_{ij})\right]$
EQV	entropy of plot valences: $N_jH_j(V_t) = N_j\log N_j - \sum_g n_{jg}\log n_{jg}$
EQI	entropy of plot invalences: $n_jH_j(v_t) = n_j\log n_j - \sum_g \left[(m-n_{jg})\log(m-n_{jg})\right]$
ESV/Q	ST entropy of species valences: $N_jH_j(V_q)/m$
ESI/Q	ST entropy of species invalences: $n_jH_j(v_q)/m$
EQV/Q	ST entropy of plot valences: $N_jH_j(V_t)/m$
EQI/Q	ST entropy of plot invalences: $n_jH_j(v_t)/m$
Diss	dissociatum: $mH_j\{\delta_\lambda^{(s)}\} = mH_j(\{A\}) + mH_j(\{B\}) + \ldots + mH_j(\{S\})$
Diss/Q	ST dissociatum: $H_j\{\delta_\lambda^{(s)}\}$
SumPosAss	sum of positive pairwise associations
SumNegAss	sum of negative pairwise associations
Diff(P-N)	difference between sum of positive and negative associations
SumPosAss/Q	ST sum of positive pairwise associations
SumNegAss/Q	ST sum of negative pairwise associations
Diff(P-N)/Q	ST difference between sum of positive and negative associations

The RSB file is the source of diacretic functions listed in Table 6. The file contains the results step by step in separated units according to species. The width of this file is 141 characters.

The output file with RSC extension includes the three most common syncretic models and their values standardized by the number of sample plots, but now based on Rényi's general entropy function. This process makes an ordering of characteristic curves by the α parameter (in addition to spatial scaling), as in case of diversity ordering (cf. Patil and Taillie, 1979; Tóthmérész, 1993, 1995). In the file there are six units according to these functions and their standardized forms, and different α values can be found in columns. α ranges from 0 to 4, and the increment is 0.1. If α=1, the program calculates the functions with Shannon entropy formula. The width of rows is 593 characters, and the file structure helps to make a three-dimensional representation. The values listed in the file can be seen in Table 7.

Table 6. Diacretic functions of RSB file. ST=standardized by number of plots.

designation	*description and formula*
Entr	local entropy of species i (or A): $mH_{ij} = mH_j(A) = m\log m - n_{ij}\log n_{ij} - (m-n_{ij})\log(m-n_{ij})$
TAss	total associativity of species A: $mI_j(\langle A\rangle) = mH_j(A) - mH_j(\{A\})$
TDiss	total dissociativity of species A: $mH_j(\{A\}) \equiv mH_j(A\|[B,C,\ldots,S]) = mH_j^{(\varphi)} - mH_j^{(\varphi\|A)}$
Diss%	total dissociativity of species A in percentage of dissociatum: $100\cdot mH_j(\{A\})/mH_j\{\delta_\lambda^{(s)}\}$
SubDiv	subflorula diversity without species A: $mH_j^{(\varphi\|A)} \equiv mH_j(B,C,\ldots,S)$
SubAss	subassociatum without species A: $mI_j([\overline{A}]) = mI_j(\lambda) - mI_j(\langle A\rangle)$
Entr/Q	ST local entropy of species A: $H_j(A)$
TAss/Q	ST total associativity of species A: $I_j(\langle A\rangle)$
TDiss/Q	ST total dissociativity of species A: $H_j(\{A\})$
SubDiv/Q	ST subflorula diversity without species A: $H_j^{(\varphi\|A)}$
SubAss/Q	ST subassociatum without species A: $I_j([\overline{A}])$

Table 7. The functions using Rényi's entropy functions, listed in RSC file. ST=standardized by number of plots.

designation	*description and formula*
FDiv	florula diversity: $mH(\alpha)_j^{(\varphi)} = m\log\sum_k (f_{jk}/m)^\alpha \Big/ (1-\alpha)$
LD	local distinctiveness: $mH(\alpha)_j([L]) = m\sum_i \left\{\log\left[(n_{ij}/m)^\alpha + ((m-n_{ij})/m)^\alpha\right]\right\} \Big/ (1-\alpha)$
Ass	associatum: $mI(\alpha)_j(\lambda) = mH(\alpha)_j([L]) - mH(\alpha)_j^{(\varphi)}$
FDiv/Q	ST florula diversity: $H(\alpha)_j^{(\varphi)}$
Ld/Q	ST local distinctiveness: $H(\alpha)_j([L])$
Ass/Q	ST associatum: $I(\alpha)_j(\lambda)$

The RSD file contains the association values. The program calculates two types of pairwise association, both of them are on the basis of the contingency table derived from the occurrences of two species. One of them is the χ^2-value (which is not part of information theory methods), and the other is the association on information theory. This latter equals to half of the G-score (cf. Zar, 1984). If interest lies in calculating the association in cases when any cell of the contingency table has zero value, the program replaces 0 with 1, so the denominator of the formula for χ^2 will not contain zero. Hereby the association will be changed a little, but if the number of sampling plots is sufficiently large, this difference is negligible. In case of the χ^2-test the significance is examined at probability levels 5%, 1% and 0.1%. Note that conventional significance test does not apply in most cases, because the requirement of independence of sampling units is not met (cf. Podani, 1984; Podani *et al.*, 1993), so the application of random references is recommended (RSH file). The RSD file is divided into units the number of which equals to the number of spatial series steps. The variables of the file are listed in Table 8. The width of rows is 86 characters.

File RSE lists the realized species combinations (florulas). In each unit, according to the spatial series steps, the florulas appear row by row. Row contains the frequency of the florula, followed by the species number of the florula, finally the code with characters 0 and 1. Further processing of data of the RSE file (e.g. collecting all florulas for all spatial series steps to apply indirect global spatial series analysis, cf. Tóthmérész, 1994a) can be performed with the COMSUM program developed by the author.

Table 8. Variables in RSD file.

designation	*description and formula*
Sp1, Sp2	series number of two compared species
A, B, C, D	fields of contingency table derived from occurrence of two species. Occurences: A: 11, B: 10, C: 01, D:00.
A*D-B*C	$ad-bc$
Chi2-Ass	$\chi^2=\frac{(m-1)(ad-bc)^2}{(a+b)(c+d)(a+c)(b+d)}$
Sign	the significance level at which the χ^2-value is significant
Inf-Ass	$mI(A,B)=m\log m+b\log b+c\log c+d\log d-(a+c)\log(a+c)-$ $-(b+d)\log(b+d)-(a+b)\log(a+b)-(c+d)\log(c+d)$

```
Name of input file: DATA.DAT
Name of parameter file: PAR
Number of quadrat in input file: 25
Number of species: 6
Dimension of sampling area: 5*5
Type of quadrat fusion: 3
Number of spatial process steps: 3
Type of random referencia: 4
Number of random referencia: 99
Frequency of most frequent and rare species: 1 and 1

  Area   QO  QR  RF  SH  BR  BD   FD/Q-Field   FD/Q-Diff   FD/Q-Aver   FD/Q-Min
-------------------------------------------------------------------------------
0.01000  25   1   1   1   1   0    4.103465   -0.150654    4.254119    3.973661
0.02000  20   2   1   1   4   1    3.546439    0.147613    3.398827    2.639354
0.04000  16   2   2   1   4   1    1.626614    0.098270    1.528344    0.337290
```

Fig. 10. A detail from the RESULTS.RSF sample output file.

The RSF, RSG and RSH files are in accordance with the RSA, RSB and RSD output files with the difference that they contain the comparison of functions with random references. The variables of these files are listed in Table 9, and an example for the RSF file can be found in Fig. 10. In a graph

representing an information statistical function, the ...-Min and ...-Max values point out the boundaries of the random envelope (cf. Fig 5a). Note that the signs of ...-Sign functions do not relate to the sign of a particular function but show that the field value was larger or smaller several times than a random value (cf. "Random references"). If value of a ...-Sign function exceeds 0.50, it means that the field value was equal to a random one's in several cases (in all cases if it is 1.00).

Table 9. Functions listed in RSF, RSG and RSH file. ST=standardized by number of plots.

designation	*description and formula*
...-Field	equal to a functions derived from field data
...-Diff	difference in a function between the field and average of random references: (...-Diff)=(...-Field)—(...-Aver)
...-Aver	average of values of random references standardized by number of sampling
...-Min	minimum value from random references
...-Max	maximum value from random references
...-Sign	*its sign*: the sign of difference between field and random values in the cases, *its value*: the value of significance level (p). $p = \frac{n - ND + 1}{n + 1}$, where n: number of randomizations, ND: number of differences between field and random values signed below
	in RSF file:
FD/Q	ST florula diversity: $H_j^{(\varphi)}$
Ld/Q	ST local distinctiveness: $H_j([L])$
Ass/Q	ST associatum: $I_j(\lambda)$
Com/Q	ST number of realized species combination: ω/m
Dis/Q	ST dissociatum: $H_j\{\delta_\lambda^{(s)}\}$
	in RSG file:
Entr/Q	ST local entropy of species A: $H_j(A)$
TAss/Q	ST total associativity of species A: $I_j(\langle A \rangle)$
	in RSH file:
Ass	pairwise association based on information theory: $mI(A,B)$ (as Inf-Ass in Table 8)

Acknowledgment

I am especially thankful to Sándor Bartha who helped my research from the initial steps in attainment knowledge of Juhász-Nagy's methods, and showed me many methodical problems. I am also very thankful to János Podani, László Gallé and László Körmöczi for recension of the manuscript, and their useful notions. I am grateful to Szilvia Fóti and Nándor Horváth for participation in the field work, and to all my collegues, firstly Miklós Dombos who, using the program, helped its development. The research was supported by the Hungarian Scientific Research Fund (OTKA F020105 and T025335).

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TISCIA 31, 85-98

THE IMPORTANCE OF NEUTRAL-MODELS IN DETECTING INTERSPECIFIC SPATIAL ASSOCIATIONS FROM 'TRAINSECT' DATA

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Bartha, S. and Kertész, M. (1998): The importance of neutral-models in detecting interspecific spatial associations from 'trainsect' data. — *Tiscia 31, 85-98.*

Abstract. We compared two Monte-Carlo randomization tests as neutral models, for measuring interspecific spatial associations. Complete randomization randomly re-allocates the individuals of each species into the spatial sample with the same abundances as in the studied sample. Thus, this separates two components of association: (1) textural, i.e. related to the species abundance distribution, and (2) structural, i.e. related to the spatial distribution of the species. Random shifts keep the spatial patterns of individual species, but change their relative positions. Thus, this method separates (1) the interspecific components of associations from (2) the intraspecific ones, randomizing the first. We also applied a new algorithm for determining the signs of pairwise associations (i.e. positive or negative). This technique is based on the comparison of the observed and simulated joint distributions of a species pair. We tested the neutral models and sign determination algorithms on multispecies circular transect ('trainsect') data. All statistics were calculated across a range of scales, i.e. the calculations were repeated at a series of sampling unit lengths. One field transect and four simulated patterns were examined. The simulated patterns, created by spatially explicit individual based model, represent known assembly rules. We concluded that circular transects are appropriate in field studies for detecting fine scale community patterns because their topology allows us to apply more types of randomizations. The separation of textural, intraspecific and interspecific effects provided us more opportunity to detect and interpret the spatial associations. The new sign determination algorithm performed better than the traditional method. The need of developing neutral models based on biological mechanisms instead of simple statistical assumptions and the dynamical relevance of textural and structural constraints are also discussed.

Keywords: circular transect, computerized sampling, information theory, randomization tests, spatially explicit Monte-Carlo simulation, sandy grasslands, scale dependence, spatial autocorrelations, textural versus structural constraints

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Introduction

Interspecific association, as a basic coenological phenomenon (Juhász-Nagy, 1980), is one of the most important aspect of community structure. It measures the tendency of species to co-occur or to avoid each other (e.g. Kershaw 1964, Greig-Smith 1983). The spatial associations of species have important consequences on their interactions, dynamics, and coexistence (Czárán and Bartha, 1992, Czárán, 1998). Therefore spatial associations are often interpreted in terms of assembly rules, i.e. pattern generating factors (Watkins and Wilson, 1992, Wilson, 1994, Wilson and Watkins, 1994, Gotelli and Graves, 1996). Despite its importance, case studies on interspecific associations are scarce (for a few exception see e.g. de Vries 1953, Agnew 1961, Fekete and Szujkó, 1973, Lepš and Buriánek, 1990, Matus and Tóthmérész, 1990, Bartha, 1992, Hauser, 1993, Margóczi, 1995). Reviewing this literature, it is difficult to generalize the results and create general rules or laws about community

structure and organization. We believe that the unsolved methodological problems associated to this field are responsible mainly for this 'state of the art'.

There are many attempts for developing new methods for detecting pairwise spatial associations (cf. Greig-Smith, 1983). However, they are often limited to a single scale (e.g. Yarranton, 1966) or they are biased by within-species autocorrelations and indirect effects of the other species (Juhász-Nagy 1980, Dale *et al.*, 1991). Recently, Palmer and van der Maarel (1995) reviewed these methodological problems and suggested to use certain types of randomizations to separate these effects. They suggested to use circular transect, called 'trainsect' to provide opportunity for several types of randomizations.

In the present study, we test their suggestions and compare the performance of different neutral models for detecting the significance of associations, and techniques for determining their positive or negative signs. For testing the performance of these methods, we use simulated data generated with known assembly rules (i.e. rules for the spatial relationships of individuals), and field data from perennial sand grasslands. We use Juhász-Nagy's information theory models (Juhász-Nagy 1967, 1980, 1984) for calculating pairwise associations. Our present study does not deal with the effect of other species on the pairwise association. However, we chose the models of Juhász-Nagy because they allow us to generalize from the pairwise relationships to multiple-, and partial associations, and to the multi-species spatial dependences in coalitions or in the whole community.

Our principal aim is to develop and test a simple technique for detecting spatial associations in the field. There is a need for simple, fast, still confident sampling designs and receipies of analyses that support huge field campaigns of data collections and allow us to compare dozens of data sets collected and analysed with the same standard technique.

Methods

Simulated patterns

To test the performance of different versions of spatial pattern analyses, two-species patterns with contrasting intra-, and interspecific spatial dependence between individuals were generated with a spatially explicit simulation model (DIVGEN1). DIVGEN1 is a simplified, one dimensional version of PATPRO (Czárán, 1984, 1993). The model generates stochastic point processes along a continuously scaled circular line in discrete time units. In the first generation, colonizing individuals appear in random positions along the transect. In the second generation, species reproduce and their offsprings disperse around the parent individuals. Distance of offsprings from their parent individual is a stochastic variable with either a Gaussian or a Poisson distribution. Survival of an offspring individual of species i, $p_{surv}(i)$, depends on the number of individuals of species i (n_i) and of species j (n_j) in a neighbourhood d. $p_{surv}(i)=g_{i,i}^{ni} \times g_{i,j}^{nj}$, where $g_{i,i}$ and $g_{i,j}$ are indicators of the intensity of interaction. Competitive effects are multiplicative. Survivorship decreases exponentially with the increasing number of individuals in the neighbourhood. Using this model with different assembly rules we created simulated patterns with different intra-, and interspecific spatial dependence of individuals

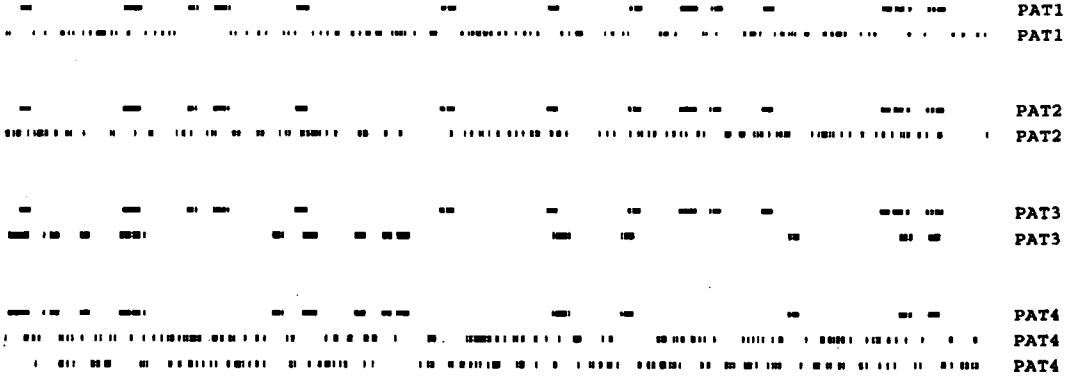

Fig. 1. Simulated spatial patterns of species along the transects (presences are marked by black dots). PAT1: species 1 is a dominant with limited dispersal, species 2 is subordinated, i.e. competitively inferior, with unlimited dispersal. PAT2: species 1 with limited dispersal, species 2 with unlimited dispersal, no competitive interaction between them. PAT3: both species with limited dispersal, no competitive interaction between them. PAT4: species 1 dominant with limited dispersal, species 2 and 3 are subordinated, i.e. competitively inferior, with unlimited dispersal. (In this paper, the association was analysed only between species 2 and 3.)

(Fig.1). The size of the plot (circular transect) was 1024 units, same as of the field sample.

Pattern 1

The first (dominant) species has limited dispersal. The second (subordinate) species disperses randomly. The dominant species has a strong competitive effect on the subordinate species. As a result, negative interspecific association is expected between the two species. The dominant species should have an autocorrelated (aggregated) pattern due to its limited dispersal while the individuals of the subordinate species could appear either random or slightly aggregated because they are restricted to the gaps between the patches of the dominant.

Pattern 2

The first species has limited dispersal, the second disperses randomly. There is no competitive effect between the species. The first species should be patchy, the second randomly distributed, and they should be spatially independent.

Pattern 3

Both species has limited dispersal, but there is no competition between them. Consequently, both species should have an autocorrelated (aggregated) pattern with no interspecific association between them.

Pattern 4

Three species were simulated here. The first (dominant) species has limited dispersal and it has the same strong competitive effect on both subordinate species. The two subordinate species could spread randomly and have no competition between them but their distributions are similarly restricted by the dominant species. We are interested in the pattern of the two subordinate species. As an indirect effect of the dominant competitor, positive interspecific association is expected between the subordinate species. Their individual patterns could be either random or slightly aggregated as they were restricted into the gaps of the dominant.

The parameters for invasion rates, fecundity of individuals, competitive strengths, and the dispersal parameter for limited dispersal are the same for the species in all simulations. The only difference was that competitive effects and/or dispersal limitations were switched on or off in different combinations.

The simulated continuous point patterns were transformed into circular transects of 1024 contiguous, discrete units. This extent and resolution are very close to the scaling applied at the field data collection. Choosing appropriate parameter values we could produce patterns with the same 12.5% frequency for each species. The species differ only in their individualistic (intraspecific) and collective (interspecific) spatial dependence.

Field data

We tested the performance of the analyses on field data from a perennial sand grassland community. The study site is a protected sand dune area near Csévharaszt, in the northern part of the Danube-Tisza Interfluve. The vegetation consists of a mosaic of woods (oak, poplar, juniper, and black locust) and grasslands (consisting of stands dominated by annuals, *Poa angustifolia*, cryptogams, *Festuca vaginata*, and *Stipa borysthenica*). Mean annual temperature is 10.2 °C, annual precipitation is 545 mm. The soil is calcareous sandy soil with shallow humic layer (<10cm) of low humus content (< 1%). The sampled grassland was a ca. 20×30 m undisturbed opening in a Juniper-Poplar wood mixed with scattered *Robinia* trees. The grassland is dominated by *Festuca vaginata*, and has a well developed cryptogam layer (mainly *Cladonia magyarica* and *furcata*). *Stipa borysthenica* is subdominant (its abundance was ca. the half of *Fectuca*). Annuals (e.g., *Viola arvensis, Polygonum arenarium, Arenaria serpyllifolia*), and an ephemeral grass, *Poa bulbosa* are also abundant. Other perennial grasses (e.g. *Koeleria glauca*) and perennial forbs (e.g. *Potentilla arenaria, Cynoglossum hungaricum, Alkanna tinctoria*) appear only sporadically. Presences of plant species were recorded along a circular belt transect of 1040 5×5 cm contiguous sampling units (52m) in June, 1995.

Sampling from transects and data analysis

The field and simulated transects served as primary samples (cf. Horváth, 1998) or primary references (sensu Juhász-Nagy, 1980) for the subsequent computerized sampling (Podani, 1984). Complete sampling (Bartha *et al.*, 1995, Horváth, 1997) was performed across a range of scales from 0.05 m to 25 m, and the resulting $s \times m$ (species by sampling units) binary matrices were analysed using information theory models (Juhász-Nagy, 1980, 1984, Juhász-Nagy and Podani, 1983). We computed associations between two species from 2×2 contingency tables applying the mutual information between the species:

$$mI(A,B) = m\log m + a\log a + b\log b + c\log c + d\log d - (a+c)\log(a+c) - (b+d)\log(b+d) - (a+b)\log(a+b) - (c+d)\log(c+d)$$

where symbols *a, b, c* and *d* correspond to the notation of the 2×2 contingency table. a is the number of sampling units where both species, *A* and *B*, are present, *d* is the number of empty quadrats. *b* and *c* note the number of quadrats, where only one species is present, *A* or *B* respectively. $m=a+b+c+d$ is the sample size. If we use the unweighted form of this equation (i.e. not multiplied by *m*), than *I(A,B)* ranges between $0 <= I(A,B) <= 1$. Thus, the equation is

$$I(A,B) = H(A)+H(B) - H(A,B)$$

i.e. the contingency information of the two-dimensional contingency table is the difference between the pooled entropy of marginals *(H(A)+H(B))* and the entropy of species combinations within the table *(H(A,B))* (Juhász-Nagy and Podani, 1983). This logic is easy to generalize to many species. Associatum refers to the overall spatial association in a community. If the community consists of s species, associatum is calculated as the contingency information of an s-dimensional contingency table, containing $2s$ cells (Juhász-Nagy, 1980, 1984).

$$I(A,B,...,S) = H(A)+H(B)+...+H(S) - H(A,B,...,S)$$

The significance of associations were detected by Monte-Carlo randomization tests. Two types of randomization were used as neutral models. (1) Complete randomization (Diggle, 1983) randomizes the positions of individuals (the presences in our case) along the transects, but the number of species and the frequency of species remains the same as in the field. (2) Random shifts (Palmer and van der Maarel, 1995, Horváth, 1998) keep the spatial pattern of each individual species, but randomize the relative (interspecific) positions of the species by shifting (rotating) it randomly along the circular transect. Thus, while complete randomization randomizes the pattern both within and between species, the random shifts randomize only the interspecific patterns.

Significance of any observed value *(I(A,B)* or *I(A,B,...S))* was calculated by comparing it with the values obtained by the Monte-Carlo randomizations, i.e. representations of the null hypothesis. The significance was expressed as the relative frequency of the randomizations resulted in higher values than the observed one. 5000 randomizations were applied in each tests. The trend of the association, i.e. whether the association is positive or negative, is given by a comparison of the expected and observed values of the joint occurrence of species A and B. (Kershaw, 1964). We compared two methods for determining the sign of association. We compared the sums of the frequencies of the diagonal cells in the 2×2 contingency table (comparing $a+d$ to $b+c$). For example, if $b+c$ is greater than $a+d$, species *A* and *B* occur together less than expected, so they are negatively associated. The other method follows the same logic but the expected frequency is obtained from the a Monte-Carlo randomization instead of calculating it from the marginal of the observed 2×2 contingency table. For example, species A and B are negatively associated if $b+c$ observed is higher than the average $b+c$ calculated from the random reference.

To avoid artefacts due to rarity and limited sample size, we analysed only the 10 most frequent species in the case of field data.

All statistics were calculated across a range of scales, i.e. the complete sampling and the calculations were repeated at a series of sampling unit lengths.

Results and discussion

Compared to other grasslands, e.g. the loess grasslands in Hungary, xeric perennial sand grasslands are considered as relatively simple systems with high stochasticity and relatively low degree of organization (Fekete, 1992). Their high diversity in life forms and ecophysiological strategies (Kalapos, 1994, Tuba *et al.*, 1998), their relatively low total biomass (Kovács-Láng, 1974), and the phenological differentiation of their species (Kárpáti and Kárpáti, 1954) suggest strong abiotic control on plant adaptation and community organization. Thus, it is supposed that there is considerable niche differentiation in this community, but the differentiation takes place rather in time (in the form of seasonal or inter-annual dynamics), than in space. We can expect low degree of spatial organization, i.e. low and non-significant spatial dependence between the species. In contrast with this expectation, we found significant and considerable departure from randomness within a wide range of scales (between 0.05m to 25m) in the case when complete randomization was used as a neutral model (Fig. 2a). This result corresponds with the large niche overlaps found by Fekete *et al.* (1995). Margóczi (1995) also obtained high spatial associations by investigating various types and successional stages of xeric sand grasslands. How ever, in our analyses, the other neutral model produced different results. Using random shifts, we found much less significant departure from randomness. The significant associations appeared only in a narrow range of spatial scales, between 0.1m and 0.4m (Fig. 2b). Table 1 shows the same con-

Table 1. Patterns of the signs of the pairwise spatial associations of the the seven most frequent species in a xeric perennial sand grassland in Csévharaszt. The signs of the associations (+,-) were determined by the comparison of the sums of diagonals ($a+d$ vs. $b+c$) of the 2×2 contingency table.

Species codes:
CLAMAG Cladonia magyarica; CLAFUR Cladonia furcata; FESVAG Festuca vaginata; STIBOR Stipa borysthenica; POLARE Polygonum aviculare; POABUL Poa bulbosa; VIOARV Viola arvensis

critical value for significance $p < 0.01$
. non-significant association
+1 positive association
-1 negative association

neutral model: complete randomization with fixed frequencies at the finest resolution

lengh of units (cm)	5	10	15	20	25	40	55	75	100	150	200	275	495	1000
species pairs														
CLAMAG x CLAFUR	.	+1	+1	+1	+1	+1	+1	+1	+1	+1	+1	.	.	.
CLAMAG x FESVAG	.	+1	+1	+1	+1	+1	+1	+1	+1	+1	+1	.	.	.
CLAMAG x STIBOR	.	.	.	.	.	.	+1	+1	+1	+1	+1	.	.	.
CLAMAG x POLARE	.	.	-1	-1	-1	-1	-1	+1	+1	+1	+1	+1	.	.
CLAMAG x POABUL	+1	-1	-1	-1	-1	-1	-1	-1	-1	-1	+1	+1	.	.
CLAMAG x VIOARV	+1	-1	-1	-1	-1	-1	-1	-1	-1	+1	+1	+1	.	.
CLAFUR x FESVAG	.	.	.	.	.	.	.	.	+1	+1	+1	.	.	.
CLAFUR x STIBOR	.	.	.	.	.	.	.	.	+1	+1	+1	.	.	.
CLAFUR x POLARE	.	.	.	.	.	.	.	.	.	+1	+1	.	.	.
CLAFUR x POABUL	+1	+1	-1	-1	-1	-1	-1	-1	-1	-1	+1	.	.	.
CLAFUR x VIOARV	.	.	.	.	.	.	.	.	.	.	+1	.	.	.
FESVAG x STIBOR	.	+1	-1	-1	.	+1	.	.	.	+1	+1	.	.	.
FESVAG x POLARE	.	.	.	.	.	.	.	.	.	+1	+1	.	.	.
FESVAG x POABUL	+1	+1	-1	-1	.	.	-1	-1	-1	+1	+1	.	.	.
FESVAG x VIOARV	.	.	.	.	.	.	.	.	.	+1	+1	.	.	.
STIBOR x POLARE	.	.	.	.	.	.	.	.	.	+1	+1	.	.	.
STIBOR x POABUL	.	.	.	.	.	.	.	.	.	.	+1	.	.	.
STIBOR x VIOARV	.	.	.	.	.	.	.	.	-1	.	+1	.	.	.
POLARE x POABUL	.	.	+1	.	+1	+1	+1	+1	+1	+1	+1	+1	+1	+1
POLARE x VIOARV	.	.	+1	+1	.	.	.	.	.	+1	+1	+1	+1	.
POABUL x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	+1	.

neutral model: random shift of species along the circular transect

lengh of units (cm)	5	10	15	20	25	40	55	75	100	150	200	275	495	1000
species pairs														
CLAMAG x CLAFUR	.	.	.	.	.	.	.	.	+1	.	.	.	.	.
CLAMAG x FESVAG	.	.	+1	+1	+1	.	.	.	.	.	.	.	.	.
CLAMAG x STIBOR	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x POABUL	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x VIOARV	+1	-1	-1	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x FESVAG	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x STIBOR	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x POABUL	+1	+1	-1	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x STIBOR	.	.	-1	.	.	.	.	.	.	.	.	.	.	.
FESVAG x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x POABUL	.	+1	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x POABUL	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POLARE x POABUL	.	.	.	.	.	.	.	+1	.	.	.	.	.	.
POLARE x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POABUL x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.

trasting differences between the patterns of significant pairwise associations of the most frequent seven species determined by the two types of randomizations. Detecting by complete randomization, all pairs of the seven species show significant associations. Significant associations are scale dependent, with considerable variation. In other studies on community structure, significant departure from randomness were rarely found (e.g., Wilson *et al.*, 1987). We think that negative results do not necessarily prove the lack of spatial organization in plant communities. They rather indicate the limitations of the applied methodology.

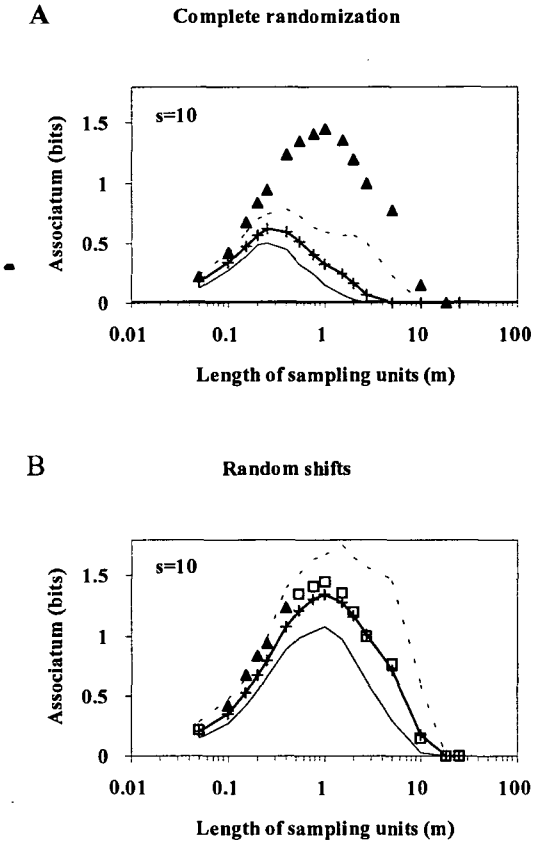

Fig. 2. Overall spatial associations (associatum) of the ten most frequent species in a xeric perennial sand grassland in Csévharaszt, detected by different neutral models: ▲ (filled triangle) significant departure of an observed value from the neutral model ($p < 0.01$), □ (empty square) non-significant observed values, + (plus) average of the random references based on 5000 Monte-Carlo randomizations, ------ maximum of the random references, —— minimum of the random references.

In studies restricted to single (often the finest) scale, or restricted to a few arbitrary chosen scales only, the majority of information about community structure may remain hidden. Scanning through a wide ranges of scales we found significant associations which do not occur at the finest scale (i.e. at the scale of the elementary 0.05 by 0.05 m sampling units). Beyond that, we had opportunity to study the pattern of associations as a function of scale.

Applying random shift as a neutral model (random reference), we found much less significant associations between species pairs. However, there was no contradiction between the two types of randomization. Results given by the random shifts appear simply as a subset of results detected by the complete randomization.

Complete randomization separates textural and structural effects on associatum, while random shifts separate intraspecific spatial dependence (autocorrelation) from the interspecific spatial dependence (interspecific association). We would expect zero associatum in case of complete randomization. However, associatum would be zero only in an ideal community where individuals would be dimensionless points and the transect would be continuous and infinite. However, vegetation forms complex mosaics, and individuals (ramets and genets) cover discrete areas of various sizes. Due to the finite and discrete nature of individuals, some (rare) combinations never appear, while other (frequent) combinations are well represented ('textural constrains', cf. Bartha, 1992). Associatum is sensitive to differences between the frequency distributions of species combinations in ideal versus real plant communities. Applying spatially explicit individual based models, recent theoretical studies suggest that textural constraints have very important dynamical consequences on species coexistence, and consequently, on the estimations of diversity (for a review see Czárán, 1998). Intra-, and interspecific spatial dependence as 'structural constraints' modify further the number and frequency of realized species combinations, thus, they modify the interactions and dynamics of populations.

It is important to note that with applying several neutral models together, we could separate these effects step by step. With these neutral models we do not simply remove the artifacts from our results, but we can distinguish and measure the relative importance of different textural and structural constraints on the dynamics of populations and communities. We emphasize that the constraints have effects on the dynamics, and not on the patterns that appear in single-time samples, which represent only "snap-shots" from dynamic processes. As we can see on Fig.2a and Fig.2b, the average random associatum is not zero in the neutral models. However, it does not simply mean that associatum is

a wrong measure because it shows 'artefact association' in case of 'randomness'. What associatum shows is the deviation of the frequency distribution of realized species combinations from an expected frequency distribution in an ideal plant community, where species can coexist in a completely unconstrained way. Because the number, frequency, and identity of realized species combinations inform us about the coexistence relations of species in a community, any deviation from the ideal (unconstrained) coexistence should contain some important information about the organization of a community.

The term "species association" in its traditional form was introduced for expressing the tendency of species to co-occur or to avoid each other (e.g. Kershaw, 1964, Greig-Smith, 1983). The significant tendencies of co-occurences are thought to form the discontinuities of the vegetation at a longer, even an evolutionary time scale. For example, these discontinuities are which can be classified as syntaxonomic units. This involves that significant associations are the most important measures of community organization. However, few studies analysed directly how effective is a certain interspecific association in determining species coexistence or community dynamics. Fig.3 shows the frequency distribution of the values of maximum associations found in the studied stand of xeric sand grassland. These values are very small comparing to the theoretical maximum of $I(A,B)$ which is 1 bit. Consequently, even if there are significant associations among species, their effects may be weak on species coexistence, i.e. the frequencies of realized species combinations differ only slightly from the random expectations (neutral models).

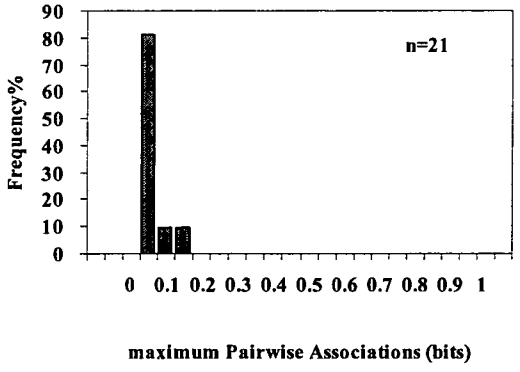

Fig. 3. Frequency distribution of the maxima of pairwise associations calculated from all the possible pairs of the seven most frequent species in a xeric perennial sand grassland in Csévharaszt. (Note the small absolute values of maxima relatively to the potential upper limit, $I(A,B)$=1.)

There are several attempts to remove the textural effects and the effects of autocorrelation as 'artefacts' from the estimated values of species associations (Dale et al, 1991, Hauser, 1993). They over-emphasize one type of structural constraint and tend to neglect the others. Although the actual abundance of species, and their intraspecific spatial patterns (autocorrelations) are individualistic properties, they have evolved in a community, so they are not independent characters. Textural and structural constraints are dynamically related, therefore the task of separating them is not simply a statistical issue.

Scale dependence and changes of the signs of associations in spatial series provide further opportunities in interpreting results on species coexistence. Kershaw (1964) and Greig-Smith (1983) expected a logical pattern of the change of the signs with increasing plot sizes. Associations start with negative values as plant individuals exclude each other at fine scales, i.e. at scales comparable to their sizes. With increasing sampling unit sizes, associations might become positive, that will disappear at even coarser scale, where both species are present in every sampling unit. From this basic logic the following variants can be expected with increasing sampling unit sizes: negative to positive to neutral, positive to neutral, negative to neutral, all neutral. There are case studies that supported these trends (e.g. Fekete and Szujkó, 1973, Bartha, 1983), while others reported more complex patterns (e.g. Hauser 1993, Podani and Czárán 1997). We found complex patterns too: e.g., neutral to positive to neutral, neutral to negative to positive to neutral, or positive to negative to positive to neutral. Comparing a large set of results (Bartha, unpublished), the most general pattern of the signs of significant associations appear to be positive to negative to positive with the increasing plot size.

Because field data are usually too complex and details about pattern generating factors (assembly rules) are unknown, we used the simulated data to test further the performance of the different types of neutral models. Similarly, we used the same sampling parameters (length and resolution of the circular transects) and the same type of data analyses because the scaling conventions of the sampling design itself could potentially introduce additional constrains on the detected frequency of species combinations.

Spatial associations between the simulated species are shown in Fig. 4. Recall that negative interspecific association is expected in case of Pattern 1 but positive interspecific association in case of Pattern 4 while species should be independent in Pattern 2 and 3. Results based on the neutral model of random shifts fit better to these

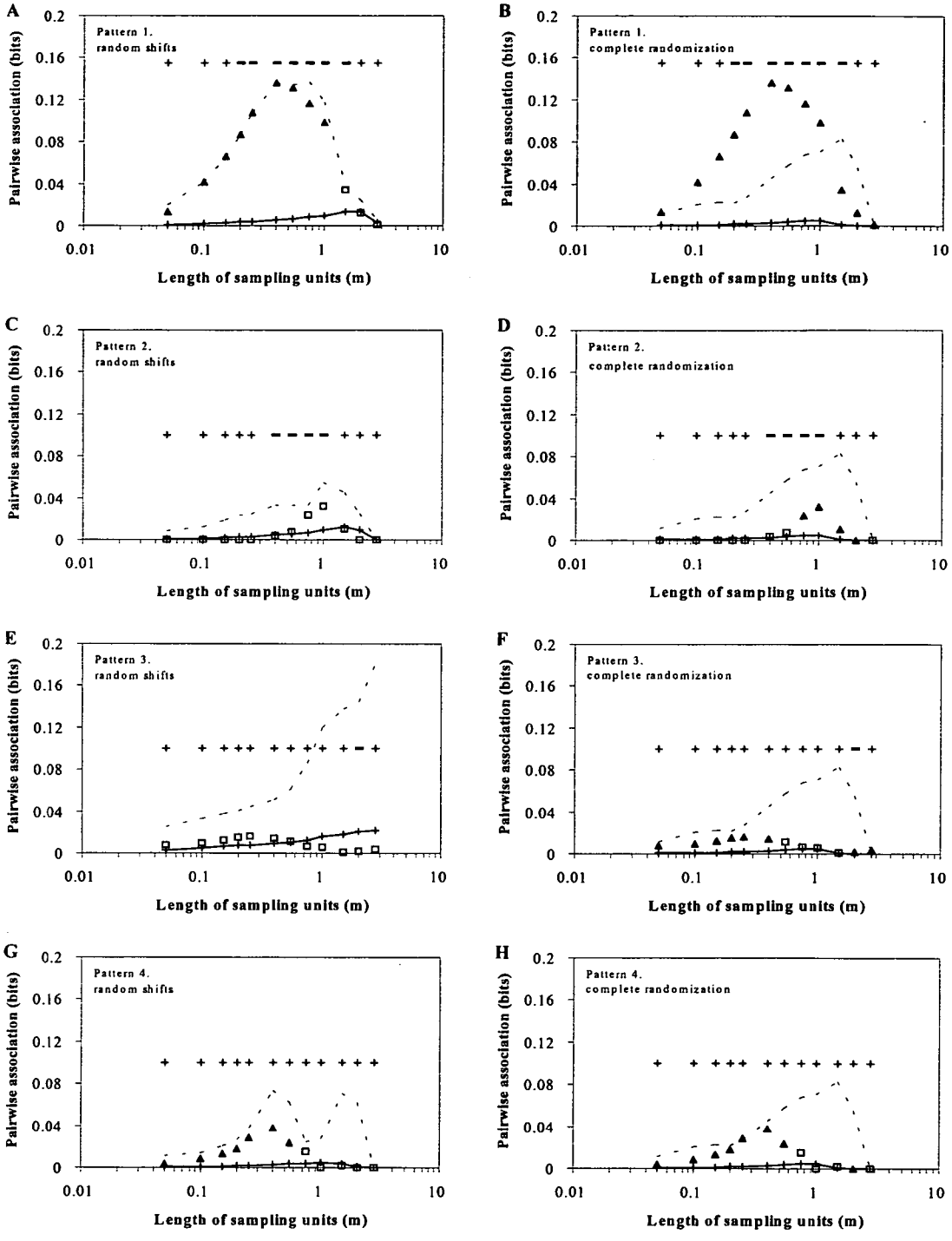

Fig. 4. Pairwise spatial associations between the simulated species. The signs of the associations (+,-) were determined by the comparison of the sums of diagonals ($a+d$ vs. $b+c$) of the 2×2 contingency table. ▲ (filled triangle) significant departure of an observed value from the neutral model ($p < 0.05$), □ (empty square) non-significant observed values, + average of the random references based on 5000 Monte-Carlo randomizations, ------- maximum of the random references, (minimum of the random references is alwais 0).

Table 2. Type of the patterns of individual species (intraspecific spatial dependence). Significance was based on 5000 complete randomizations.

Simulation	Species	Status of the species	Type of pattern p<0.01	Intraspecific spatial dependence
PAT1	Species 1	Dominant	aggregated	yes
PAT1	Species 2	Subordinated	random	no
PAT2	Species 1	Dominant	aggregated	yes
PAT2	Species 2	Co-dominant	random	no
PAT3	Species 1	Dominant	aggregated	yes
PAT3	Species 2	Co-dominant	aggregated	yes
PAT4	Species 2	Subordinated 1.	random	no
PAT4	Species 3	Subordinated 2.	random	no

expectations. There are no significant spatial dependence in Pattern 2 and 3 (Fig. 4c and Fig. 4e) while significant positive associations are found in Pattern 4 (Fig. 4g). There are positive associations in Pattern 1 at smaller plot sizes and negative associations at medium plot sizes (Fig. 4a). The majority of results corresponds to the assembly rules of the simulations, however the positive associations found at fine scales in Pattern 1 contradict to our expectation. The results based on the complete randomization are more complex and more difficult to interpret. For Pattern 4, the results are the same as the results by the random shifts, even the random envelopes (minimum and maximum values of randomizations) produced by the two types of neutral models are different (Fig. 4h). However, significant associations are found in all the other simulated patterns and the signs are both positive and negative, depending on the scale (Fig. 4b, Fig. 4d, and Fig. 4f). Difference of the results calculated with the two types of neutral models can be attributed to the fact that complete randomization also refers to the intra-specific spatial dependence (autocorrelation) of species. As it was shown in Fig. 1, the dominant species was patchy (aggregated) in all patterns, the subordinate species was patchy only in Pattern 3. In the other cases, the subordinate species was distributed by unlimited dispersal, which could produce either random or slightly segregated patterns, depending on the competitive effect of dominant.

To test the above expectations about the individualistic patterns (i.e. intraspecific spatial dependence) of species, we calculated the probability of finding a species in a quadrat as a function of quadrat sizes. If a species is aggregated, it appears in the sample with lower probability than in case of randomness (Fig. 5). Table 2 summarizes the results. These correspond to our expectations according to the assembly rules of the simulation. In the cases when competition occurs, segregation of the subordinate species from the dominant do not produce patchy distribution, because the frequencies of the subordinate species are low (12.5 %). However, limited dispersal always produces significant aggregations. Comparing the significant associations detected by the two neutral models, there are additional significant associations in the results obtained by complete randomizations. If only one of the species is aggregated (Fig.4b and Fig.4d), then the additional significant associations appear only at coarse scales. But, if both species are aggregated, the associations are significant at almost all scales (Fig. 4f). It is clear that intra-specific spatial dependence changes the probability of the species to appear in a sampling unit (cf. Fig. 5). However, the consequence of this change appears in the probability of co-occurence of species, too. If at least one of the species becomes aggregated, the probability of co-occurences will decrease, as it was shown by applying the neutral model of complete randomization.

Are the significant associations artefacts in Fig. 4d and Fig . 4f? We think they are not. We extend the concept of association to the intraspecific level, thus, the individuals are associated if their probability to appear in a sampling unit are significantly different from a random expectation. We emphasize that association between individuals changes their interactions. A second question is that how individuals can be classified into groups (e.g. taxons or functional types etc.). To solve this task we can separate the within-, and between-group associations with appropriate neutral models.

In Fig. 4 we depict the signs of $I(A,B)$ at all scales, disregarding if they show significant associations or not. Signs were determined by comparing the $a+d$ vs $b+c$ sums calculated from the

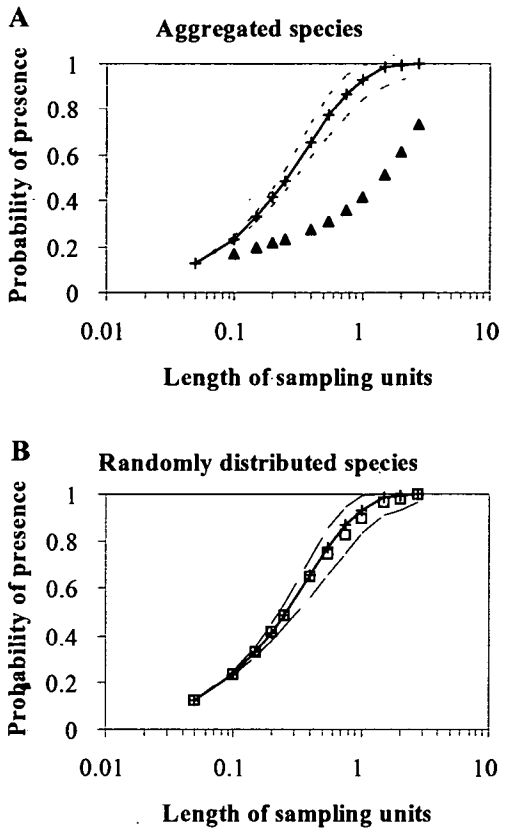

Fig.5. Detection of the spatial pattern of individuals species. An example with the two simulated species in Pattern 1. A, aggregated pattern of dominant species, b, random pattern of subordinated species. ▲ (filled triangle) significant departure of an observed value from the neutral model ($p < 0.01$), □ (empty square) non-significant observed values, + average of the random references based on 5000 Monte-Carlo randomizations, ------- maximum and minimum of the random references.

diagonals of the 2×2 contingency table of observed data. The signs follow the same positive to negative to positive pattern with the increasing plot sizes in each simulated transects. This pattern is similar to the one found in the field data (see Table 1), and might be simply a direct consequence of increasing the plot sizes in the spatial series. We expect that $a+d > b+c$ at very small plot sizes, because d is very frequent, i.e. there are many empty plots. At large plot sizes, close to the minimum area of the two-species assemblage, a is very frequent, thus $a+d > b+c$ again. In the contrary, at intermediate plot sizes, $b+c$ might be greater than $a+d$. The intervals of scales where signs change vary from pattern to pattern, but the logic is the same. This pattern of positive to negative to positive signs is often invisible, because significant associations may appear only in a limited interval of scales. The effects of changing the frequencies of species combinations with increasing plot sizes might mask the "real" trends of positive and negative associations. Textural effects might override the real tendencies of species to co-occur. It may result in seemingly illogical patterns of the signs of associations (e.g. Fig. 4a) that are difficult to interpret, or at least, there is a danger of misinterpretation.

To avoid these effects, we suggest a second type of algorithm for determining the signs of the associations. Here the observed sums of diagonals were compared to the average sums of diagonals calculated from the Monte-Carlo random references (neutral models). Table 3 shows the signs of significant associations detected by this method. This result is easier to interpret than the result obtained by the first method. The positive signs disappeared from the simulated Pattern 1. Using random shift as a neutral model, Pattern 4 shows only positive associations, which corresponds to our expectation. There is a change of the signs from positive to negative in case of complete randomization, when within-species spatial dependence is also detected. It is reasonable, because aggregation in the original species pattern reduces the probability of finding a species in a sampling unit. For example, if both species are aggregated but they are independent from each other (Pattern 3), the relative frequency in a (both species are present) will be smaller, the frequency in d (both are absent) will be higher than the random expectation created by complete randomization (Fig. 6a and Fig. 6d). Relative frequencies in *b* and *c* (only one species is present) are lower than the random expectation at finer scale and then become higher at coarser scale (Fig. 6b and Fig. 6c). All these effects together result in the positive to negative change of the signs of the significant associations.

Recalculating the signs of associations with the second algorithm, we found more reasonable and less controversial patterns in case of the field data too (Table 4). When we apply random shift as neutral model, there are either only positive or only negative associations along the spatial series. Applying complete randomization, there is the same positive to negative change of the signs as found in the case of simulated pattern. Exceptionally, negative to positive to negative pattern appears if there are other components of associations beyond the intraspecific. Applying random shifts as neutral models significant associations show a coalition structure. There are negative associations between the dominant grasses *Festuca vaginata* and *Stipa borysthenica*, as well as between the matrix-forming *Festuca* and the gap-species *Poa bulbosa*. Annuals

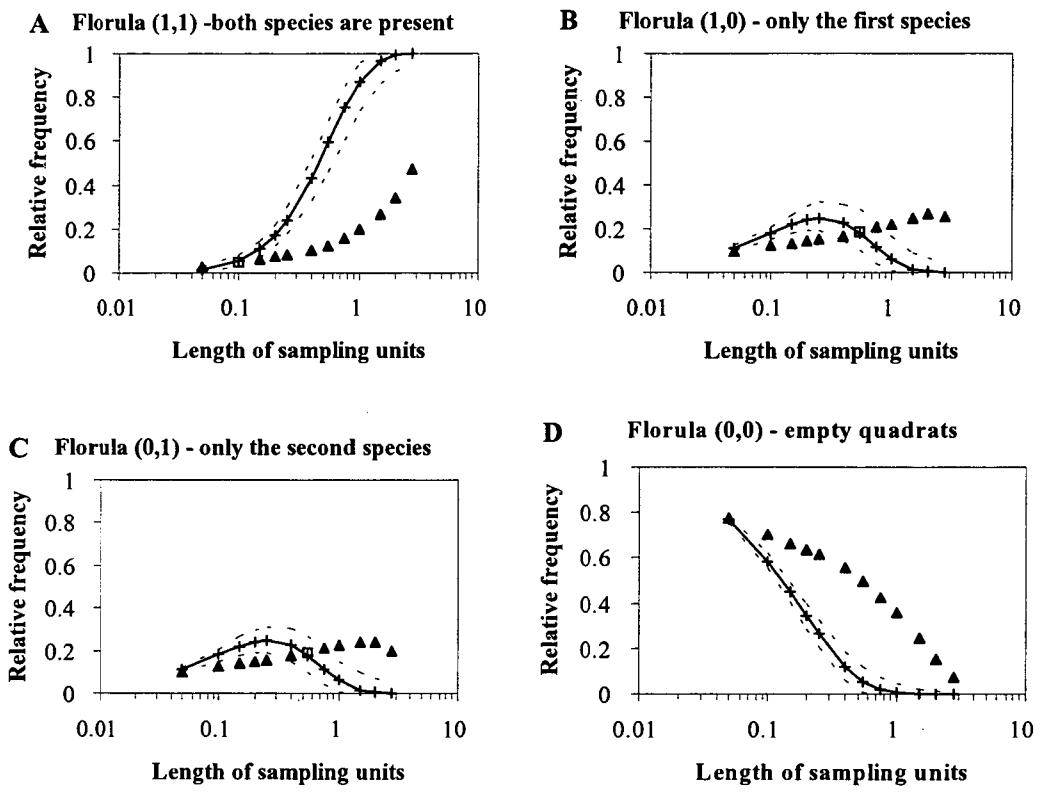

Fig. 6. The effect of within-species spatial dependence (autocorrelation) on the spatial patterns of species combinations. An example with Pattern 3., where both species are aggregated due to their limited dispersal, however, there are no interaction between them. ▲ (filled triangle) significant departure of an observed value from the neutral model ($p < 0.05$), □ (empty square) non-significant observed values, + average of the neutral model (5000 complete randomizations), -------- maximum and minimum of the random references.

Table 3. Patterns of the signs of the pairwise spatial associations of the species in the simulated patterns. The signs of the associations (+,-) were determined by the comparison of the observed vs. the average random sums of diagonals of the 2×2 contingency table.

```
critical value for significance p < 0.05
    . non-significant association
   +1 positive association
   -1 negative association

neutral model: complete randomization with fixed frequencies at the finest resolution

 lengh of units (cm)   5  10  15  20  25  40  55  75 100 150 200 275
simulations
  Pattern 1           -1  -1  -1  -1  -1  -1  -1  -1  -1  -1  -1  -1
  Pattern 2            .   .   .   .   .   .   .  -1  -1  -1  -1   .
  Pattern 3           +1  +1  +1  +1  +1  +1   .   .   .  -1  -1  -1
  Pattern 4           +1  +1  +1  +1  +1  +1  +1   .   .   .  -1   .

neutral model: random shift of species along the circular transect

    lengh of units (cm)   5  10  15  20  25  40  55  75 100 150 200 275
simulations
  Pattern 1           -1  -1  -1  -1  -1  -1  -1  -1  +1   .   .   .
  Pattern 2            .   .   .   .   .   .   .   .   .   .   .   .
  Pattern 3            .   .   .   .   .   .   .   .   .   .   .   .
. Pattern 4           +1  +1  +1  +1  +1  +1  +1   .   .   .   .   .
```

Table 4. Patterns of the signs of the pairwise spatial associations of the the seven most frequent species in a xeric perennial sand grassland in Csévharaszt. The signs of the associations (+,-) were determined by the comparison of the observed vs. the average random sums of diagonals of the 2×2 contingency table.

critical value for significance p < 0.01
. non-significant association
+1 positive association
-1 negative association

neutral model: complete randomization with fixed frequencies at the finest resolution

lengh of units (cm)	5	10	15	20	25	40	55	75	100	150	200	275	495	1000
species pairs														
CLAMAG x CLAFUR	.	+1	+1	-1	-1	-1	-1	-1	-1	-1	-1	.	.	.
CLAMAG x FESVAG	.	+1	+1	-1	-1	-1	-1	-1	-1	-1	-1	.	.	.
CLAMAG x STIBOR	.	.	.	.	.	.	-1	-1	-1	-1	-1	.	.	.
CLAMAG x POLARE	.	.	+1	-1	-1	-1	-1	-1	-1	-1	-1	-1	.	.
CLAMAG x POABUL	-1	+1	+1	-1	-1	-1	-1	-1	-1	-1	-1	-1	.	.
CLAMAG x VIOARV	-1	+1	+1	+1	+1	-1	-1	-1	-1	-1	-1	-1	.	.
CLAFUR x FESVAG	.	.	.	.	.	.	.	.	-1	-1	-1	.	.	.
CLAFUR x STIBOR	.	.	.	.	.	.	.	.	-1	-1	-1	.	.	.
CLAFUR x POLARE	.	.	.	.	.	.	.	.	.	-1	-1	.	.	.
CLAFUR x POABUL	-1	+1	+1	+1	+1	-1	-1	-1	-1	-1	-1	.	.	.
CLAFUR x VIOARV	.	.	.	.	.	.	.	.	.	.	-1	.	.	.
FESVAG x STIBOR	.	-1	-1	-1	.	-1	.	.	.	-1	-1	.	.	.
FESVAG x POLARE	.	.	.	.	.	.	.	.	.	-1	-1	.	.	.
FESVAG x POABUL	-1	+1	+1	+1	.	.	-1	-1	-1	-1	-1	.	.	.
FESVAG x VIOARV	.	.	.	.	.	.	.	.	.	-1	-1	.	.	.
STIBOR x POLARE	.	.	.	.	.	.	.	.	.	-1	-1	.	.	.
STIBOR x POABUL	.	.	.	.	.	.	.	.	.	.	-1	.	.	.
STIBOR x VIOARV	.	.	.	.	.	.	.	.	-1	.	-1	.	.	.
POLARE x POABUL	.	.	+1	.	+1	+1	+1	+1	+1	-1	-1	-1	-1	-1
POLARE x VIOARV	.	.	+1	+1	.	.	.	.	.	-1	-1	-1	-1	.
POABUL x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	-1	.

neutral model: random shift of species along the circular transect

lengh of units (cm)	5	10	15	20	25	40	55	75	100	150	200	275	495	1000
species pairs														
CLAMAG x CLAFUR	.	.	.	.	.	.	.	.	+1	.	.	.	.	.
CLAMAG x FESVAG	.	.	+1	+1	+1	.	.	.	.	.	.	.	.	.
CLAMAG x STIBOR	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x POABUL	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAMAG x VIOARV	-1	-1	-1	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x FESVAG	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x STIBOR	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x POABUL	-1	-1	-1	.	.	.	.	.	.	.	.	.	.	.
CLAFUR x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x STIBOR	.	.	-1	.	.	.	.	.	.	.	.	.	.	.
FESVAG x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x POABUL	.	-1	.	.	.	.	.	.	.	.	.	.	.	.
FESVAG x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x POLARE	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x POABUL	.	.	.	.	.	.	.	.	.	.	.	.	.	.
STIBOR x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POLARE x POABUL	.	.	.	.	.	.	.	+1	.	.	.	.	.	.
POLARE x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POABUL x VIOARV	.	.	.	.	.	.	.	.	.	.	.	.	.	.

are positively associated to *Poa bulbosa*, while negatively associated to lichens. Lichens are positively associated to *Festuca*. The whole structure corresponds to our previous experiences about the ecophysiology, population biology, and larger scale coenological preferences of species in xeric perennial sand grasslands.

Conclusions

Pairwise spatial association of species is a measure to express the difference between frequency distributions of species combinations in an observed and in an ideal community. The traditionally used ideal distribution represents a community where all species can completely coexist, i.e. the probabilities of species combinations are determined only by the abundance of species.

There are several factors that might cause a deviation from this ideal case.

1, *Textural constraints* appear due to the fact that stands of plant communities and individual plants (or ramets) are *finite and discrete entities*. The sampling operations emphasize this finite and discrete character of natural communities when the limited extent and resolution of the sample reduce further the freedom of species combinations. Consequently, some rare species combinations may never appear in a limited, finite sample, while the combinations of the abundant species might be over-represented. Similarly, if the number of species is relatively high, the number of potential species combinations might exceed the size of the sample. In this case, the limited size of the sample puts constraints on the number and frequency of realized species combinations, that result in deviation from the ideal case. Important to emphasize that textural constraints are not simply sampling artefacts due to our limited sampling efforts. In nature, frequency of realized species combinations will also differ from an ideal (continuous and infinite) case due to natural scaling parameters (limited extent of vegetation stands and given natural scales defined by plant morphology) in a community.

Students of community structure usually pay little attention to textural constraints or they regard them as some unwelcome noise or bias from the real biological patterns and mechanisms. Considerable attempts have been made to remove these effects of the textural constraints from the analyses to get really „pure, biologically reasonable" results. However, because textural constraints effect species interactions and community dynamics as well, neglecting or disregarding them might cause serious biases in our understanding of community organization.

2, *Structural constraints* appear because of the spatial dependence between individuals. *Within-species spatial dependence*, i.e. non-random spatial distribution of individuals of the same species might appear due to population level mechanisms (e.g. limited dispersal of propagules, patterns of vegetative growth and reproduction or preference of individuals to certain patches of a heterogeneous habitat). *Inter-specific spatial dependence* can be the consequence of direct interaction of species (e.g. competition, parasitism, mutualisms) or due to indirect effect, i.e. the common reaction to other species or limiting environmental factors. In each case, spatial dependence changes the frequency of species combinations either directly, by changing the probability of the occurence of a given species combination, or indirectly, by changing the individualistic patterns, i.e. the individualistic probability of the occurence of a species in a sampling unit.

3, We use the term *'constraints'* instead of 'effects' or 'contributions' to emphasize the *dynamic aspects* and dynamic consequences. From a dynamic point of view, zero association corresponds to the conditions that are assumed in a mass-based equilibrium model (e.g. Lotka-Volterra models) (cf. Czárán, 1998). In any more realistic model of plant community dynamics, association means that the behaviour of the species differ from what we expect directly from their overall abundances. The associated species co-occur or interact more or less frequently due to several textural and structural effects that constrain their behaviour. We emphasize the need of developing a well articulated set of neutral models that help to separate the different type of biologically relevant constraints. As a first attempt, we used here two different types of neutral models in parallel.

4, We propose to use (1) the complete randomization model to separate textural and structural constraints, and (2) the random shifts to distinguish intra-, vs. interspecific spatial dependence within structural constraints. We also suggest that detecting signs of significant associations, we should compare the relative frequencies of relevant species combinations between the observed data and the actual neutral model. In all cases, the application of spatial series is important and inherent in the analyses.

Our simulation study proves that with these methods one can detect much details than with the traditionally used statistical method. These methods have the advantage of simplicity and easy use. However, neither complete randomization nor random shifts are perfect from a biological point of view. By artificial setting of the resolution of complete randomization we might cut a plant

individual into pieces and randomize along the transects. On the other hand, random shift keeps the individual pattern constant during the randomization involving the irrealistic assumption that pattern of one species was developing independently from the other species. The major problem lies in the tradition of developing static neutral models with statistical approaches disregarding that the majority of biological processes and mechanisms that are relevant only in dynamical context (Geoffrey M. Henebry, personal communication). Future neutral models for understanding plant community structure should be based on thorough knowledge about the dynamics of the morphogenesis of plants and the synmorphogenesis of vegetation.

Acknowledgements

We are grateful to Beáta Oborny and Gábor Fekete for helpful comments on the manuscript. This study was supported by the Hungarian Scientific Researc Fund (OTKA T016225 to S. Bartha, and T021166 to M. Kertész).

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TISCIA 31, 99-106

DATA TO KNOWLEDGE OF HUNGARIAN DINOPHYTA SPECIES III. CONTRIBUTION TO THE DINOPHYTA TAXA OF KÖRÖS AREA I.

I. Grigorszky, K. T. Kiss, F. Vasas and G. Vasas

Grigorszky, I., Kiss, K.T., Vasas, F. and Vasas, G. (1998): Data to knowledge of Hungarian Dinophyta species III. Contribution to the Dinophyta taxa of Körös area I. — *Tiscia 31, 99-106.*

Abstract. Dinophyte species were investigated during this study from 28 sites in Körös area. Samples were taken from different oxbow-lakes, canals, and rivers. 30 taxa were identified, including 27 ones that were not previously reported from the Körös area and two from Hungary. New taxa for the Hungarian algal flora are *Cystodinedria inermis,* and *Peridiniopsis kevei* (*P. kevei* is a new freshwater species - Grigorszky *et al.* in print). The rare and valuable new species from Körös area are *Glenodiniopsis steinii, Gymnodinium fuscum, G. hiemale, Katodinium vorticella, Peridiniopsis cunningtonii, P. kevei, Peridinium volzii, Sphaerodinium cinctum, Woloszynskia pseudopalustris.* Four different forms of *Ceratium hirundinella* were recognized, including forma *furcoides,* forma *gracile,* forma *piburgense* and forma *robustum.*

Keyword: Dinophyta, Körös area, ***Ceratium, Glenodiniopsis, Gymnodinium, Katadinium, Peridiniopsis, Peridinium, Sphaerodinium, Woloszynskia.***

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Introduction

Only a few paper were published about the algal flora of the Körös area, same on diatoms, some on desmids and chlorophytes (Koren 1883, Szalai 1942, Kol 1954, Uherkovich 1963, Vasas 1980a, 1980b, 1986). Three Dinophyta species were reported from this area: *Ceratium cornutum* (Uherkovich 1968), *Ceratium hirundinella* (Kol 1954) and *Glenodinium gymnodinium* (Szalai 1941). Concerning on this later species there is a doubt of identification, missing any drawing, micrograph or plate tabulation (unknown species name - perhaps missprint).

Dinophyta species are a distinctive group of unicellular protists recognized by their swimming pattern (spinning while advancing due to transverse and longitudinal flagella), usually golden-brown pigmentation, centrally located nucleus with permanently condensed chromosomes and the lacking of histones. Dinophyta species can be divided into two groups:

(i) those with a cellulose wall composed by plates („armored"), and

(ii) those apparently lacking a rigid wall („naked").

Determination of armored Dinophyta species must be confirmed by the tabulation of plates, the unarmored species are confirmed by inner structure and cell shape however, certain key features can be recognized in some species which aid in their identification. (Kofoid 1909, Lefévre 1932, Huber-Pestalozzi 1950, Bourrelly 1968, Starmach 1974, Spector 1984, Popovsky and Pfiester 1990). The objective of the present study is to report on Dinophyta species found in the Körös area and provide a short descriptions and a key, which can be useful to algologists working with phytoplankton samples (Table 1).

Materials and methods

Quantitative phytoplankton samples were taken by 1 l bottles and for qualitative analyses net samples — pore size 10 μm — from the open water of oxbow lakes, canals, rivers and squeezing from the submerse vegetation (sampling sites on Fig. 1). Most part of sampling were made between 1989 and 1994. One half of samples were preserved with Lugol's iodine and the other half were examined immediately upon return to the laboratory. Line drawings were based on sketches made during microscopic observations and from micrographs.

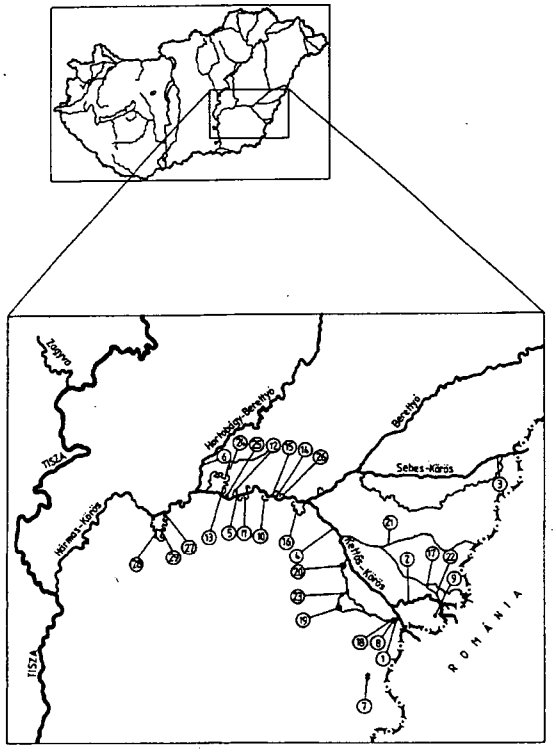

Fig. 1. Sketch map of sampling sites. 1. Fehér-Körös, 2. Fekete-Körös, 3. Sebes-Körös, 4. Kettős-Körös, 5. Hármas-Körös, 6. Hortobágy-Berettyó main canal, 7. Kétegyházi inland water reservoire, 8. Gyula inner lake, 9. Dénesmajori lake, 10. Torzsási-backwater, 11. Gyoma inner backwater, 12. Templom-Bónom-Socózugi backwater, 13. Peresi-backwater, 14 Siratói-backwater, 15. Siratói-backwater (end of the oxbow), 16 Félhalmi-backwater, 17. Gyepeses-canal, 18. Élővíz-canal (Gyula), 19. Élővíz-canal (Békéscsaba), 20. Élővíz-canal (Békés), 21. Határér, 22. Kopolya (Sarkad), 23. Gerlai-backwater, 24. Malomzugi-backwater, 25. Kecskészugi-backwater, 26. Kecsegészugi-backwater, 27. Szarvasi-backwater(Szivornya), 28 Szarvasi-backwater (HAKI halrács), 29. Szarvasi-backwater (Anna-liget)

The description of different oxbows and backwaters were found in book of Pálfi (1995). For identification the books of Starmach (1974) and Popovsky and Pfiester (1990) were first of all used.

Results

Dinophyte cells are considered to have a typical ventral and dorsal view. The mid-cell cingulum divides the cell into an upper part (epitheca, epicone) and lower part (hypotheca, hypocone). Thus, the cell may be viewed from four directions: ventral, dorsal, apical and antapical. Thecate (armored) Dinophyta species have a cellulose wall divided into plates and their taxonomy is based on the number and arrangement of the plates. Kofoid (1909) proposed a code system for the plate arrangement, socalled tabulation. Plates are often in concentric rows above and below the cingulum. The ventral plate in series is the first plate and plates are numbered counterclockwise on epitheca and anticlockwise on hypotheca.

The series of plates closest to the apex is designated apical and has a single prime (') mark after the number. Precingular plates have two prime following the number, postcingular three prime, and antapical four prime. Plates between the apical and precingular series are anterior intercalary (a), and plates between postcingular and antapical series are posterior intercalary (p).

Plate tabulations are always included in species descriptions (e.g., 4', 3a, 7'', 5''', 2'''' for *Peridinium cinctum).* Non-thecate (naked) Dinophyta species lack a well developed cellulose wall and their taxonomy is based on cell shape, pigmentation, presence of an eyespot (stigma), and motility. During this study 30 taxa were identified: 24 armored, and 6 naked, of which 27 are new records for the Körös area, two new species for Hungary (Fig. 2). Most of the taxa recorded here have distinctive features which facilitate their identification.

We present here a key based on the species of Dinophyta species found by the author and does include all previously reported species. (Table 1.)

Ceratium Shrank 1793

Ceratium hirundinella is characterized by one apical, one antapical, and one or two postcingular horns. *C. hirundinella* as having recognized different forms (Huber-Pestalozzi 1950) varying number of postcingular horns. The *Ceratium* cells are golden yellow with thick plates displaying reticulate ornamentation. Plate plate-tabulation is 4', 5'', 5''', 2''''. Length 188- 322 μm. Distinctive phytoplankton and the most commonly reported freshwater Dinophyta species. This species is distinguished from C. *cornutum* by the straight position of the apical horns. (Fig. 2/1, 5).

(i) Cells with 3 horns under optimal conditions:

Ceratium hirundinella forma *furcoides* (Levander) Schoeder 1920 (Fig. 2/1) Cells are relatively

narrow — up to 60 µm — and long — 180-350 µm — with 3 horns under optimal conditions. The apical horn is in the same angle as the antapical horn. The species was found: 25. collecting site. (The numbers sign the sampling sites on Fig.1.)

(ii) Cells with 4 horns under optimal conditions:

C. hirundinella forma *robustum* (Amberg) Bachmann 1911 (Fig. 2/2) has a smaller body volume than the *Ceratium hirundinella* forma *hirundinella* form. The antapical horn is long and slightly divergent, the postcingular horns are half in length of the antapical one. The length of the cells is 168-320 µm. The species was found in 21., 22. collecting sites.

Ceratium hirundinella forma *gracile* Bachmann 1911 (Fig. 2/3) The cell has one or two downward pointing postcingular horns. It is similar to forma *hirundinella,* differing in the direction of horns. The length of the cells is 147-238 µm. The species was found in 24. collecting site.

Ceratium hirudinella forma *piburgense* (Zederbauer) Bachmann 1911 (Fig. 2/4) The outer antapical horn and the postcingular horns are divergent. The cells are 163-210 µm long and 40- 52 µm wide. The species was found in 8., 14., 15. collecting sites.

Ceratium cornutum (Ehrenbergh) Claparede and Lachmann 1858 (Fig. 2/5) has a relatively short, wide and curved apical horn. The apical horn directed an angle from the longitudinal axis. On the hypotheca two unequal horns are visible, the smaller one can be reduced or the lacking of it sometimes typical at low temperature conditions. The cells are 97-150 µm long and 48-75 µm wide. The species was found in 8., 9., 16., 29. collecting sites.

Cystodinedria Pascher 1944

The *Cystodinedria* species has two main life cycle stages: (i) gymnoid phase and (ii) cystodinedroid stage. The species can be identified only in cystodinedroid stage. In this stage the cells are oval in shape and attached to a substrate. The substrate are mainly filamentous Cyanobacteria or Chlorophyta. Sometimes numerous spines are visible on the surface of the cell. The chloroplasts are mainly discoid but sometimes absent.

Cystodinedria inernis (Geitler) Pascher 1944 (Fig. 2/6) is a parasitic taxon, approximately oval except for flattening where it is appressed to a host cell. It may be recognized by its golden coloration and large nucleus. The species were found on filaments of *Cladophora* sp. The cells are 40-48 µm long and 33-36 µm wide. The species was found in 9. collecting site.

Glenodiniopsis Woloszynska 1916

Cells are oval without apical pore. The chloroplasts are numerous and parietally situated. Cells six to eight postcingular plates on hypotheca. There are no stigma. Numerous red corpuscles can be present within the cytoplasm. The cingulum is deep and spirals to the left.

Glenodiniopsis steinii (Lemmermann) Woloszynska 1916 (Fig. 2/7). The cells are somewhat oval and flattened dorso-ventrally. The apical pore is absent. The plate arrangement is asymmetric. The plate formula is 4', 4a, 8'', (6-8)''', 2''''. The cells are 36-48 µm long and 32-46 µm wide. The species was found in 28. collecting site.

Gymnodinium Stein 1878

Gymnodinium is a genus of naked Dinophyta species with the cingulum in a median position. They must be examined and sketched while alive and swimming, because upon death they form featureless spheres (the only way to distinguish *Gymnodinium* from thin walled *Glenodiniopsis, Peridiniopsis* and *Woloszynskia).* The species are differentiated by the shape of the epicone and hypocone, details of the sulcus, presence a stigma, and the color of chloroplasts. Species can be photosynthetic with yellow-gold or blue-green chloroplasts, or they can be non-photosynthetic and colorless, or they may have accumulation bodies of various colors (yellow, orange, red).

Gymnodinium fuscum (Ehrenbergh) Stein 1878 (Fig. 2/8). The epicone is dome-shaped and the hypocone forming an inverted cone a slightly produced tip. The numerous chloroplasts are radially arranged. The cells are 53-75 µm long and 43-56 µm wide. The species was found in 9. collecting site.

Gymnodinium hiemale (Schiller) Popovsky 1984 (Fig. 2/9) is a non-photosynthetic species, its sulcus extends to antapex, the nucleus is in the hypocone, and there can be red inclusion bodies. The specimens from the Körös area are are larger (average length 21 µm) than those described in the literature (16 µm). The cells are 18-25 µm long and 12-26 µm wide. The species was found in 9. collecting site.

Gymnodinium palustre Schilling 1891 (Fig. 2/10) is an autotrophic, holophytic species. The epicone can be twice in lenght of the hypocone. Numerous chloroplasts are parietally arranged. The cells are 36-48 µm long and 20-31 µm wide. The species was found in 9. collecting site.

Gymnodinium uberrimum (Allman) Kofoid and Swezy 192 1 (Fig. 2/11). The cells are broadly sphaerical and little flattened dorso-ventrally. The epicone is rounded or bell-shaped. The hypocone is highly variable in size and form. Numerous chloroplasts are radially arranged. The cells are 38-52 µm long and 30-40 µm wide. The species was found in 5., 6., 8., 16., 25. collecting sites.

Katodinium Fott 1957

Cells are spherical, oval or mushroom shaped. The cingulum is anteriorly placed and slightly spiral. The cell wall thin and colorless. The species mainly colorless. Fott (1957) placed from the *Massartia* Conrad 1926 genus to *Katodinium* genus.

Katodinium vorticella (Fig. 2/12) are usually colorless species, if chloroplasts present there are less than 10, which are relatively small and green or grey. Numerous reddish droplets can be present in the cytoplasm. If the shape of these droplets oval, it is a sign of the saprotrophic nutrition. If number of red droplets one or two and the shape is rectangular the cell is in sexual reproduction process. The cells are 18.5-33 µm long and 18-30 µm wide. This is a common species in different peat bogs, ponds and pools. The species was found in 8., 23. collecting sites.

Peridiniopsis Lemmermann 1904

Bourrelly (1968) transferred one part of *Glenodinium* species with known plate tabulations into the genus *Peridiniopsis;* it remains a highly variable genus (3-5', 0-la, 6-7'', 5''', 2'''').

Peridiniopsis cunningtonii Lemmermann 1907 (Fig. 2/13). Cells are elongated. From two to six spines are on the hypntheca. Chloroplasts are numerous and oval. The plate formula is 4', la, 6'', 5''', 2'''', or 5', Oa, 6'', 5''', 2''''. The cells are 32-48 µm long and 27-46 µm wide. The species was found in 2., 21., 26., 28. collecting sites.

Peridinopsis elpatiewskyi (Ostenfeld) Bourelly 1968 (Fig. 2/14). Cells are pentangular. Several spines or teeth-like projection may be present on the hypotheca. There are numerous chloroplasts. The plate formula is 4', Oa, 7'', 5''', 2''''. The cells are 29-44 µm long and 27-42 µm wide. The species was found in 13., 16. collecting sites.

Peridiniopsis kevei Grigorszky, Vasas F. et Klee 1997 (Fig. 2/15). The plate tabulation : 3', 1 a, 6'', 5''', 2'''' ; the species is unicellular; theca and plate arrangement of glenoid and young cell not visible with light microscope; the average lenght is 35 µm, 37 µm width; epitheca vary in shape from acute to a little blunt from; cingulum median and deep, narrower than sulcus; sulcus is deep, and is not reach to epitheca; some short spines (cristae) are on the edge of the sulcus, transverse flagellum as long as cingulum; longitudinal flagellum trailing body by less than one cell length; cells with numerous golden-brown chloroplasts generally located peripherally, their shape vary from ovoid to elongate; stigma sometimes present; nucleus large, with conspicuous chromosomes, usually located in hypotheca; pore exist at the apical end; 1'''' antapical plate has a relatively long tapering spines; some short spines (cristae) are on the edges of antapical plates. The species was found in 1., 2., 3., 4., 5., 6., 10., 11., 14., 15., 17., 18., 19., 20. collecting sites.

Peridiniopsis polonicum (Woloszynska) Bourrelly 1968 (Fig. 2/16) can be recognized by its conical epitheca, rounded hypotheca, and squared shape 1a plate. The plate pattern is 4', 2a, 7'', 5''', 2''''. The cells are 41-52 µm long and 37-39 µm wide. The species was found in 13., 16. collecting sites.

Peridinium Ehrenberg 1830

Peridinium is defined by its plate tabulation: 4', 2-3a, 7'', 5''', 2''''. Species differ from each other in the number of intercalary plates, apical symmetry, and the presence or absence of an apical pore. Most species are found as minor components of the phytoplankton although occasionally one species can be completely dominated in a pond or lake.

Peridinium achromatium Levander 1932 (Fig. 2/17). Cells are rhomboidal and flattened dorsiventrally. The plate formula is 4', 3a, 7'', 5''', 2''''. Chloroplasts are absent. The cells are 40-53 µm long and 36-49 µm wide. The species was found in 15. collecting site.

Peridinium aciculiferum Lemmermann 1900 (Fig. 2/18). The cells are elongated. Usually spines are found on the hypotheca. The plate formula is 4', 3a, 7'', 5''', 2''''. The apical pore is present. The sulcus reaches the epitheca. The cells are 32-45 µm long and 20-40 µm wide. The species was found in 13., 14., 15., 28. collecting sites.

Peridinium bipes Stein 1883 (Fig. 2/19) has an apical pore, its cingulum is offset a cingulum width, and it is ventrally concave. Its plate pattern is 4', 3a, 7'', 5''', 2''''. The cells are 45-67 µm long and 41-64 µm wide. Our specimens lack the typical paired antapical flanges. It looks like a *P. willei* with an apical pore. The species was found in 6., 9., 11., 17. collecting sites.

Peridinium cinctum Ehrenbergh 1838 (Fig. 2/20). The cells are sphaerical. The cingulum extends further into the epitheca. Chloroplasts are numerous and parietally arranged. Plates are thick. Plate formula is 4', 3a, 7'', 5''', 2''''. The cells are 43-59 µm long and 42-53 µm wide. This species

widespread in oxbows and canals in summer months. The species was found in 10., 26. collecting sites.

Peridinium inconspicuum Lemmermann 1899 (Fig. 2/21) is a small, approximately pentagonal cell with an apical pore, yellow-gold chloroplasts, and an approximately equatorial cingulum. Cells may have hypothecal spines. Plate pattern is 4', 2a, 7'', 5''', 2''''. The cells are 18-22 µm long and 15-19 µm wide. The species was found in 1., 2., 3., 6., 10., 11., 17., 18., 19., 20., 21., 27., 28., 29. collecting sites.

Peridinium goslaviense Woloszynska 1916 (Fig. 2/22). The cells are egg or pear-shaped. One large spine present on the hypotheca. The plate formula is 4', 2a, 7'', 5''', 2''''. The cells are 28- 34 µm long and 22-32 µm wide. The species was found in 9. collecting site.

Peridinium palatinum Lauterborn 1896 (Fig. 2/23). The cells are ovoid. The absence of pore and the plate formula: 4', 2a, 7'', 5''', 2'''' are typical for this species. The plate arrangement is asymmetrical. Sutures are concave. The cells are 37-43 µm long and 24-39 µm wide. This species an common winter species in Körös area. The species was found in 8., 14., 15., 28. collecting sites.

Peridinium umbonatum (Fig. 2/24) is a golden to dark brown cell, it is round in apical or antapical view (i.e., no dorsoventral compression), and wider than long. Some cells have red accumulation bodies. Its apical and intercalary plates are in an symmetrical arrangement and there is apical pore. Plate pattern is 4', 2a, 7'', 5''', 2''''. The cells are 28-37 µm long and 32-45 µm wide. It was common in the studied area, sometimes found in bloom condition. The species was found in 5., 11., 12., 17., 18., 19., 20., 23., 24., 29. collecting sites.

Peridinium volzii Lemmermann 1906 (Fig. 2/25) has a plate pattern similar to P. *willei* with apical intercalary plates in a symmetrical arrangement, but the cell is less compressed, and the 1' plate smaller than 7''. The cells are round in ventral view, somewhat dorsoventrally compressed, with a defined sulcus reaching the antapex, and thick plates with reticulate ornamentation; plate pattern is 4', 3a, 7'', 5''', 2''''. The cells are 42-50 µm long and 35-44 µm wide. The species was found in 11., 12., 27. collecting sites.

Peridinium willei Huitfeld-Kaas 1900 (Fig. 2/26) is a fairly large, golden brown species with distinctive flanges extending from apical plate boundaries, cingulum, and posterior borders, no stigma, concave ventral surface, and the 1st apical plate (1') is large. Its apical and intercalary plates are in a symmetrical arrangement and there is no apical pore. Plate pattern is 4', 3a, 7'', 5''', 2''''. The cells are 48-58 µm long and 49-52 µm wide. It was found fairly commonly throughout the Körös area. The species was found in 13., 23., 24. collecting sites.

Sphaerodinium Woloszynska 1916

Sphaerodinium cirnctum (Ehrenbergh) Woloszynska 1916 (Fig. 2/27). The cells are oval. The epitheca and hypotheca are equal in size. Plate formula: 4', 4a, 7'', 6''', 2''''. Apical pore is present. The cells are 28-34 µm long and 22-30 µm wide. The species was found in 29. collecting site.

Woloszynskia genus Thompson 1950

The cell wall is composed of very fine, numerous platelets, which are usually hardly or not seen during ligh microscopic (LM) investigations. Many species have been described, but it is only possible to unambigouously determine 5-7 species.

Woloszynskia ordinata (Skuja) Thompson 1950 (Fig. 2/28). The cells contain less than five, big chloroplasts. The size of platelets is the bigest one among the *Woloszynskia* species. The cingulum is broad and deep. The cells are 15-20 µm long and 13-18 µm wide. The species was found in 14., 15. collecting sites.

Woloszynskia pascheri (Suchlandt) v. Stoch 1973 (Fig. 2/29). The cells is varied in shape and in size. Regular hexagonal platelets cover the cell. The cells are 15-42 µm long and 24-39 µm. The species was found in 12. collecting site.

Woloszynskia pseudopalustris (Woloszynska) Kiselev 1954 (Fig. 2/30). The hypovalva is „excavated". The morphology and arrangement of platelets are not well documented. Chloroplasts are numerous and are in parietal position. The cell are 34-45 µm long and 34-42 µm wide. The species was found in 11. collecting site.

Discussion

The presence of Dinophyta species, other than that of *Ceratium hirundinella*, is probably underreported in the literature because of both the inherent difficulty in determination of genera and species, and an old and scattered literature. Armored Dinophyta species require elucidation of the plate pattern and comparison to reponed patterns. Naked Dinophyta species require immediate examination. During this study a few taxa with thin thecae were found but not identified because of insufficient material and lack of definitive characteristics. During our investigation 30 species were found in Körös area and two of them are new species for Hungary: *Peridiniopsis kevei, Cystodinedria inermis*. Up to now 32 freshwater Dinophyta species were known form Hungary and only three species were known from this area. In our

Table 1. Key to the Dinophyta species of Körös area.

1a. Vegetative cells free-swimming 2
1b. Vegetative cells attached on filamentous algae or submerse vegetation ..... *Cystodinedria inermis*
2a. Cells unarmored 3
2b. Cells armored 7
3a. Cingulum is equatorial 4
3b. Cingulum is not equatorial. ..... *Katodinium* vorticella
4a. Sulcus extends into the epicone more than 1/3 of length of epicone ..... *Gymnodinium uberrimum*
4b. Sulcus does not extend into the epicone 5
5a. Cells are spherical ..... *Gymnodinium hiemale*
5b. Cells are not spherical 6
6a. Chloroplasts are parietally arranged ..... *Gymnodinium palustre*
6b. Chloroplasts are radially arranged ..... *Gymnodinium fuscum*
7a. The cells have numerous, small, similar size plates 8
7b. Plates not numerous, and dissimilar in size 10
8a. Less then five, big chloroplats are present. ..... Woloszynskia *ordinata*
8b. Numerous small chloroplasts are present 9
9a. The hypovalva is „excavated" ..... *Woloszynskia pseudopalustris*
9b. The hypovalva is rounded ..... *Woloszynskia pascheri*
10a. Cells with one apical and 1-3 antapical horns 11
10b Cells without homs 15
11a. Apical horn straight compared with the longitudinal axis 12
11b. Apical horn directed at an angle from the longitudinal axis ..... Ceratium cornutum
12a. Cells with 3 horns ..... *Ceratium hirundinella f. furcoides*
12b. Cells with 4 horns 13
13a. Antapical horn and postcingular horn are not divergent ..... *Ceratium hirundinella f. gracile*
13b. Antapical horns or postcingular horns are divergent 14
14a. Antapical horn is parallel with the apical horn, but the postangular horns are divergent ..... *Ceratium hirundinella f. robustum*
14b. Antapical horn is not parallel with the apical horn ..... *Ceratium hirundinella f. piburgense*
15a. Five postcingular plates (5''') 17
15b. Six or seven postcingular plates (6''' or 7''') 16
16a. Apical pore present ..... *Sphaerodinium cinctum*
16b. Apical pore absent ..... *Glenodiniopsis stenii*
17a. Cells have zero or one intercalary plate 27
17b. Cells have two or three intercalary plates 18
18a. Apical pore present 22
18b. Apical pore absent 19
19a. Cells have two intercalary plates ..... *Peridinium palatinum*
19b. Cells have three intercalary plates 20
20a. 3a intercalary plate does not reach the 4'' precingular plate 21
20b. 3a intercalary plate reaches the 4'' precingular plate ..... *Peridinium cinctum*
21a. 1' apical plate is pentangular ..... *Peridinium volzii*
21b. 1' apical plate is quadangular ..... *Peridinium willei*
22a. Cells have two intercalary plates 23
22b. Cells have three intercalary plates 25
23a. Cells have one spine on the hypotheca ..... *Peridinium goslaviense*
23b. Cells without spines or have lots of spines on the hypotheca 24
24a. The cells longer than wider ..... *Peridinium umbonatum*
24b. The cells approximately as long as wide or little wider ..... *Peridinium inconspicuum*
25a. Chloroplasts are present 26
25b. Chloroplasts are absent ..... *Peridinium achromatium*
26a. 3a - intercalary plate - does not reach 4'', precingular plate ..... *Peridinium bipes*
26b. 3a - intercalary plate - reaches 4'', precingular plate ..... *Peridinium aciculiferum*
27a. Cells with 7'', precingular plates 28
27b. Cells with 6'', precingular plates 29
28a. Cells with 0a, intercalary plate ..... *Peridiniopsis elpatiewskyi*
28b. Cells with 1a, intercalary plate ..... *Peridiniopsis polonicum*
29a. Cells with 3', apical plates ..... *Peridiniopsis kevei*
29b. Cells with 4' or 5'' apical plates ..... *Peridiniopsis cunningtonii*

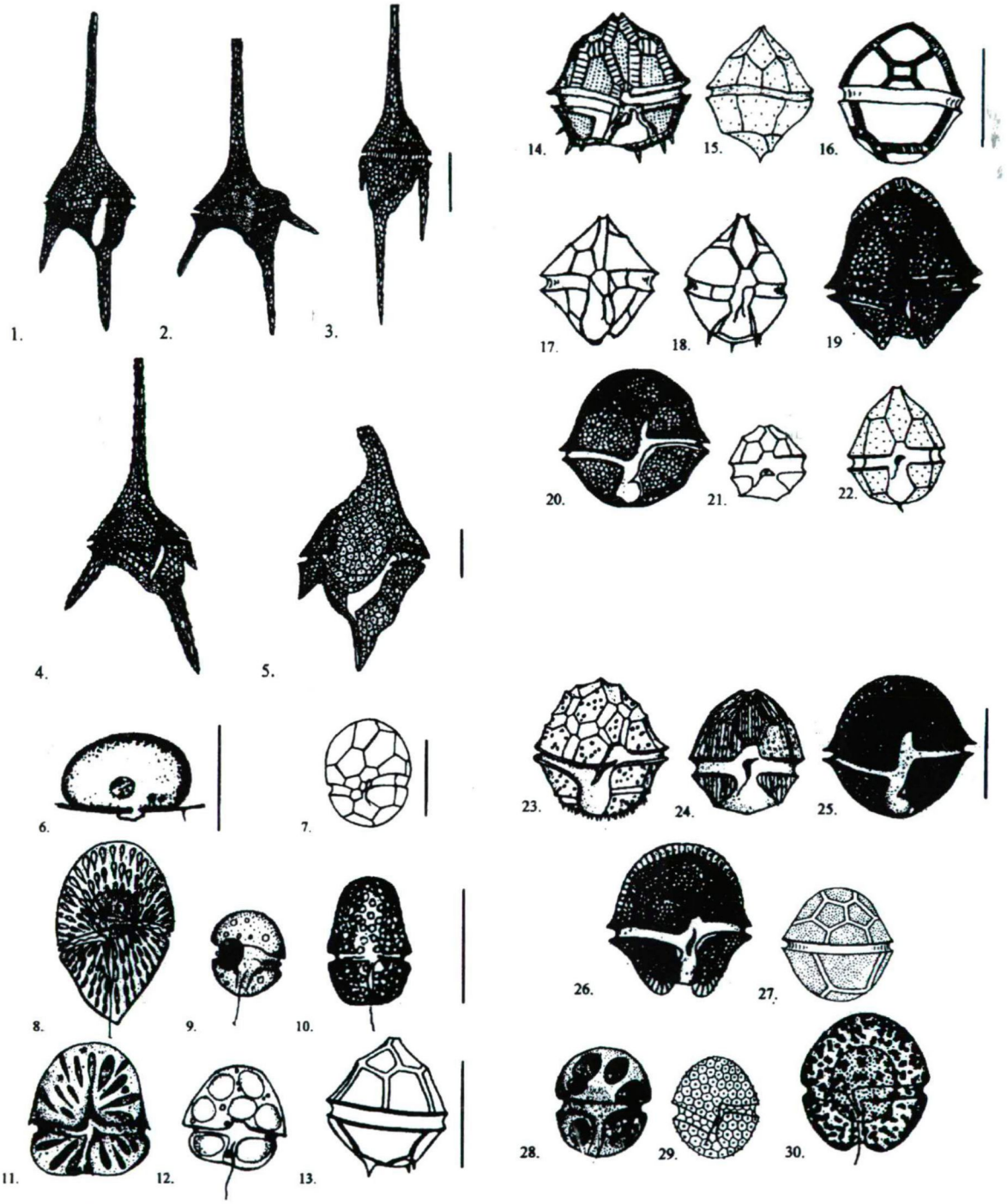

Fig. 2. Dinophyta species from Körös area. Bars beside figures correspond 30 µm. 1.: Ceratium hirundinella f. furcoides. 2.: Ceratium hirundinella f. robustum. 3.: Ceratium hirundinella f. gracile. 4.: Ceratium hirundinella f. piburgense. 5.: Ceratium cornutum. 6.: Cystodinedria inermis. 7.: Glenodiniopsis stenii. 8.: Gymnodinium fuscum.. 9.: Gymnodinium hiemale. 10.: Gymnodinium palustre. 11.: Gymnodinium uberrimum. 12.: Katodinium vorticella. 13.: Peridiniopsis cunningtonii. 14.: Peridiniopsis elpatiewskyi. 15.: Peridiniopsis kevei. 16.: Peridiniopsis polonicum. 17.: Peridinium achromatium. 18.: Peridinium aciculiferum. 19.: Peridinium bipes. 20.: Peridinium cinctum. 21.: Peridinium inconspicuum. 22.: Peridinium goslaviense. 23.: Peridinium palatinum. 24.: Peridinium umbonatum. 25.: Peridinium volzii. 26.: Peridinium willei. 27.: Sphaerodinium cinctum. 28.: Woloszynskia ordinata. 29.: Woloszynskia pascheri. 30.: Woloszynskia pseudopalustris.

opinion although the Körös area is full of interesting and wonderful waters (rivers, canals, oxbow-lakes, dead-arms) from algological point of view, but it is not a unique place in Hungary in that point of view, as well. The lack of investigations resulted that this area was „poor" in Dinophyta species. Probably this is true for other part of Hungary. The authors hope that this work will be useful to algologists working with phytoplankton samples, find and want to identify or to know more about these species.

Acknowledgements

This study was supported by the Hungarian Scientific Research Fund (OTKA No. F 16455, 23761).

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Tiscia intends to facilitate the wide range publication of scientific results. From this year, summary of technical reports and other research activities that were published only in few copies will be released in the section „Report review".

ECOLOGICAL STATE ASSESSMENT IN MÁRTÉLY LANDSCAPE-PROTECTION AREA

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Kovács, É., Gallé, L., Dombos, M., Györffy, Gy., Hornung, E., Körmöczi, L., Margóczi, K. and Rudner, J. (1998): Ecological state assessment in Mártély Landscape-protection Area. — *Tiscia 31, 107-109.*

Abstract. The paper summarises the results of the studies on natural conditions in Mártély Landscape-protection area. We presented general information about the survey of natural conditions. A large-scale vegetation map was given with the botanical-floristical characterisation of habitat types. The studied reference groups of arthropods were: *Gastropoda, Isopoda, Collembola, Homoptera, Auchenorrhyncha, Cicadinea, Coleoptera, Caraboidea, Hymenoptera, Formicoidea.* We described the vegetation of the studied areas and emphasised importance of some Arthropod species. The last part of the paper contains proposals for nature conservation.

Key words: state assessment, arthropods, vegetation

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This paper summarises the main results of the technical report on a state assessment compiled by Kovács (1996).

The 42 paged report is divided into six chapters. In the first section it gives a short review on scientific researches performed in the landscape-protection area, with special regard to the activity of Tisza-research Working Committee. It emphasises the scientific and nature protection importance of this region from two point of view: this area is part of the ecological corridor formed by Tisza-valley and it can be regarded as the natural laboratory of community disturbances owing to the natural disturbation of regular floods.

The following three chapters give general information about the survey of natural conditions: the list of sampling areas, sampling data and the description of sampling methods are published in them. The botanical research carried out during the survey of natural conditions has two important way:

(1) We prepared the vegetation map of the Mártély Landscape-protection Area. This large-scale map can serve as the basis of every further survey, mainly for detecting changes in vegetation.

(2) We characterised in detail the vegetation in sampling areas of invertebrate fauna. We chose the sampling areas of invertebrate fauna in such a way that these areas represented both the typical natural habitats of Mártély Landscape-protection Area and the frequently occurring more disturbed habitats as well. We based the selection of sampling areas on plant associations because according to our previous studies the sensitivity of vegetation to habitat heterogeneity is more finer that those of the majority of animal communities, so habitats discriminated by vegetation generally represent sufficiently fine division also for animal communities. The chosen sampling areas of invertebrate fauna: Babos forest,

Körtvélyesi-Petres forest, Hunyadi hillock and Téreriverside oak-forest. For the survey of natural conditions we studied reference species and reference groups because the study of complete biocenoses technically can not be performed. Besides vascular plants the chosen reference groups were: *Gastropoda; Isopoda; Collembola; Homoptera: Auchenorrhyncha, Cicadinea; Coleoptera: Caraboidea; Hymenoptera: Formicoidea* and vertebrate fauna.

The fifth chapter gives the results of the survey of natural conditions. Botanical results include the botanical characterisation of sampling areas, lists of plant species and any further information collected during the field-work. Readers can find detailed description about the main sections of the landscape-protection area: Ányás island, Kutyafenék, Körtvélyes island and Barci-medow. Planted forests, mostly hybrid poplar woods cover large areas; they are disturbed to a great degree since they are under intensive treatment of forestry. Main species of native forests are: white willow (*Salix alba*), white poplar (*Populus alba*), black poplar (*Populus nigra*), *Fraxinus angustifolia,* but also occurs *F. pennsylvanica* and pedunculate oak (*Quercus robur*). Forests of nature species are found on the eastern part of Ányás island and the southern part of Körtvélyes island (otherwise they remained only in patches in other sections of the landscape - protection area); an old soft-wooded gallery forest also survived in the latter territory. In the undergrowth *Alopecurus pratensis* and *Typhoides arundenacea* grass species are dominant, plants of one-time hard-wooded gallery forest also occur in it, e. g. lily of the valley *(Convallaria majalis).* Unfortunately the common weed ragweed (*Ambrosia elatior*) lives in vast number in some places. There are many disturbance-indicator and adventive plants in the shrub level, first of all dewberry*(Rubus caesius)* and bramble species (*Rubus spp.*); *Fraxinus pennsylvanica* and *Amorpha fruticosa* are also widely spread. The territory bordered by Körtvélyes-backwater is perhaps the most valuable section of the landscape-protection area, particularly wet grasslands spiced with old willow trees and poplar groups are remarkable: grasses of *Alopecurus pratensis, Typhoides arundenacea, Bolboschoenus maritimus, Glyceria maxima* and *Schoenoplectus lacustris.* Ploughlands can be found in Kutyafenék and on Barci-medow, of course these are the less natural habitats; holiday camp also reaches the northern part of the former section.

Zoological results partly include species lists of reference groups and the quantitative characterisation of reference species, partly include the characterisation of sampling areas emphasising important data in the respect of indication, degradation and biogeography of species.

Notable *Gastropoda* species found in the landscape-protection area are: *Vallonia pulchella, V. ennensis* and *Vertigo antivertigo*; their occurrences refer to undisturbed habitats.

From *Isopoda* group the records of *Hyloniscus riparius* refer to wetter and less disturbed conditions.

Remarkable *Collembola* records are: *Orchesella* and *Entomobrya* species, they indicate intensive leaf-litter decomposition. *Entomobrya atrocincta* is found only in non-degraded habitats.

Species from *Cicadinea* group are: *Euscelidius variegatus* which is rare in Hungary and has southern range. *Criomorphus williams* is also noteworthy species, it were known up till now only from England and Kazakhstan.

Besides *Carabidae* species living typically on flood plains there are also three protected species of this taxon living in the landscape-protection area: *Carabus cancellatus tibiscinus* (endemism characteristic of the Great Hungarian Plain), *Carabus granulatus granulatus* and *Carabus clathratus auraniensis.* The quite rare *Calosoma inquisitor* also occured, it lives in oak-forests. *Dyschirius globosus* prefers wet habitats, while *Calathus fuscipes, Pseudoophorus rufipes* indicates degradation. A scarce *Brachinus psophia* were also recorded.

Formicoidea species form a species assemblage typical of flood plain forests. *Myrmica rugulosa, Myrmica specioides* are remarkable species generally living on loess-soils in the southern regions of the Great Hungarian Plain.

We made multivariate ordination analysis (PCoA) on assemblages of 17 insect groups from which we obtained valuable scientific results about similarities and differences between distribution patterns of these taxa. Results of the survey of natural conditions in Mártély Landscape-protection Area provided new data confirming our knowledge - originated from studies of larger scale - about the role of habitats connecting with Tisza-river (habitats of Tisza-valley and dam system): these territories serve as important species pool and species propagating areas. Our wide-ranging researches on the southern part of the Great Hungarian Plain also showed the existence of some animal and plant species living exclusively along Tisza-river or in nearby habitats (e. g. *Messor structor* ant species indicating warm and dry habitats).

In order to illustrate the foregoing we represented the species distributions of some invertebrate taxa on UTM-maps; the maps concerning the Mártély Landscape-protection Area are also included in the report.

The last chapter contains proposals for nature conservation. these suggestions touch upon among others the replacement of planted forests by native tree species at least after final cutting; the importance of continuous change of water in oxbow lakes; the rehabilitation of ploughlands into nearly natural habitats; the restoration of traditional methods of cultivation; the prevention of further expansion of holiday resort and the necessity of its canalization.

Acknowledgement

This study was partly supported by the Kiskunsági National Park and by the Hungarian Scientific Research Fund (OTKA No. T 020149).

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Nyomás és kötés készült az OFFICINA Nyomda Kft.-ben
6728 Szeged, Dorozsmai út 35. 99-159
Felelős vezető: dr. Kékes Tiborné ügyvezető